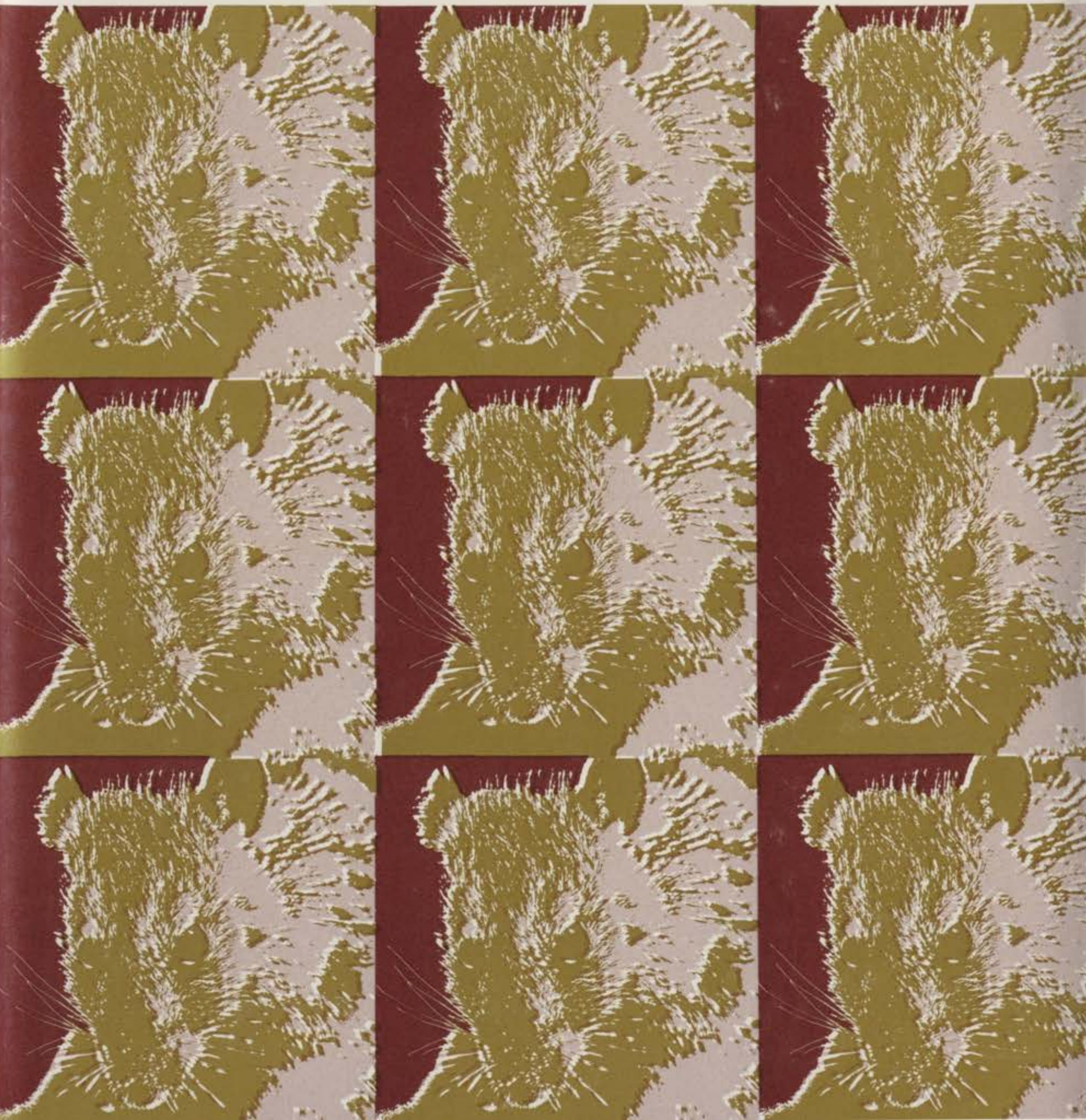
The Rat

A Study
in Behavior

Revised Edition
S. A. BARNETT



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Barnett's classic study, originally published as *A Study in Behaviour*, has had a major influence on teaching and research in the behavioral sciences. The author's purpose is to present some of the principles of ethology, the science of animal behavior, primarily from studies of a single species, the "Norway" rat. This edition includes a number of new topics, additional text figures and photographs, an enlarged bibliography, and a revised glossary.

Barnett's work is unique because it covers recent findings on one mammalian species from three areas of study: experimental psychology, ethology, and behavioral physiology. He recognizes the need to amalgamate studies of both laboratory and wild rats, and to include the results of observations in the field, to arrive at a balanced account of rat behavior. Barnett, therefore, complements his extensive laboratory researches with descriptions of the behavior of wild rats. The principal topics covered include: movement in the living space, feeding behavior, social and reproductive behavior, the analysis of instinct, the analysis of learned behavior, motivation and drive, and the brain's function in behavior.

Barnett's experience as a teacher has enabled him to write an unusually comprehensive and lucid text, suitable for students of psychology, zoology, and medicine. As a reference work on a single organism, it will be indispensable to researchers.

S. A. BARNETT was educated at Magdalen College, Oxford. He was senior lecturer in the Glasgow University Zoology Department and is now professor and head of the department of zoology at The Australian National University. He is the author of *"Instinct" and "Intelligence."*

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Revised Edition

The Rat
A Study in Behavior

S. A. Barnett

Australian National University Press
Canberra, 1976

S. A. Barnett is professor of zoology at the Australian National University. He is the author of *The Human Species* (5th edition, 1971) and *"Instinct" and "Intelligence"* (1967); co-author of *Rodents of Economic Importance in India* (1975); and editor of *A Century of Darwin* (1958) and *Ethology and Development* (1973).

The present book is a revision of *A Study in Behaviour,* published in London in 1963 and later reissued in the United States as *The Rat: A Study in Behaviour.*

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Preface

Nullius addictus iurare in verba magistri.

The first English edition of this book had the excessively non-committal title, *A Study in Behaviour.* The present title states more clearly what the book is about. My intention is still to present some of the findings of ethology, that is, of the science of animal behavior, principally from studies of a single species. This is made possible largely by the concentration of behavioral research on laboratory rats; but a balanced account could be attempted only because something is now known of the behavior of wild rats.

As the epigraph implies, this book is not written from the point of view of any one school or theoretical system. The choice of examples represents my admiration for research whose authors range from neurophysiologists to naturalists. A witty reviewer of the first edition described how he had shown the book to colleagues of diverse specialities. Each was kind enough about the book as a whole. Each had severe doubts about the section on his own subject: he felt, naturally (and rightly), that he could have done it better. Nevertheless, the response to the first edition suggests that an attempt at synthesis by a single author can still be useful.

I have assumed that communication about behavior is aided by rigorous definition of important technical terms, and by holding to each definition once given. The definition of "definition" is discussed in an appendix. No doubt I have often failed to keep to my own principles. A disadvantage of being clear is that one must sometimes be clearly wrong, but it is better to risk that than to resort to obscurity.

The attempt to be rigorous has obliged me sometimes to criticize opinions no longer held by their original authors or by present authority. Obsolete theories and notions often reverberate in teaching when their usefulness has been exhausted. Examples include the concept of innate behavior current in the 1950s, and the textbook story of conditional reflexes, which has persisted for decades. None of my criticisms is directed *ad hominem.*

I have tried to give clear acknowledgment wherever I have quoted the observations or ideas of others, except where recent comprehensive reviews have been available. In the passages in which only general references are given, the original sources must be sought in the reviews. In most parts of the book each account of particular researches is preceded by an author's name and ends with a numerical reference to the bibliography. Occasionally, the reference is given in the caption of an accompanying text figure.

I am indebted to Michael Abercrombie for suggesting that this book should be written. R. A. Hinde kindly read most of the typescript, and made valuable criticisms. Help with portions of the first edition was generously given also by G. C. Kennedy and Joseph Schorstein. Much of the second edition was read by D. G. Fraser and J. L. Smart, parts by John O'Keeffe and P. E. Cowan. I am very grateful to all these colleagues for their advice, even when I have not taken it. Special acknowledgment is due to Gabriel Donald for his drawings of wild rats in action. For her work on the typescript of the second edition, and especially on the bibliography, I am much indebted to Jenny Bowers.

Canberra
September 1973

In my view, aiming at simplicity and
lucidity is a moral duty of all intellectuals:
lack of clarity is a sin, and
pretentiousness is a crime.

K. R. Popper

Statement of Themes

1

. . . whenever we propose a solution to a problem we ought to try as hard as we can to overthrow our solution, rather than defend it. . . . Other people, fortunately, will supply the criticism for us if we fail to supply it ourselves. Yet criticism will be fruitful only if we state our problem as clearly as we can and put our solution in a sufficiently definite form.

K. R. Popper

1.1 Natural History

A much esteemed experimental psychologist once published a denunciation of the excessive use of tame rats in laboratory studies of behavior. His article, inspired by a work of Lewis Carroll, was entitled "The Snark was a Boojum"; it suggested that comparative psychology had softly and suddenly vanished away under predation by *Rattus norvegicus* var. *albinus* [73].

It is nevertheless possible to illustrate many of the principles of ethology from one genus, or even one species, only. Accordingly, this book is mainly concerned with *Rattus norvegicus* Berkenhout: in its wild form this is the common "brown" rat of Europe, North America, and elsewhere (figure 1, plate 1). It is sometimes called the Norway rat. Albino and other tame varieties of this species have been used in laboratories for more than half a century, and much of the book describes experiments on them. Linnaeus (1707–78) called *R. norvegicus* the huge mouse, or *Mus decumanus*, and so allied it more closely, than we do today, to that other universal pest, the house mouse, *Mus musculus*. E. L. Trouessart (1842–1927) compromised with the generic name, *Epimys*, which implies a superior mouse, but today the common rat is unequivocally *Rattus*—a distinction it shares with nearly three hundred other alleged species [214]. In French it is *le surmulot*, in German, *die Wanderratte*—no doubt from its rather recent invasion of Europe from Asia. As a result of its immigrations of the past few centuries, it is now present in most large human communities in cold and temperate lands and in much of the subtropics. It has almost completed its occupation of North America, and is present in much of Central and South America. Only the efforts of pest controllers mar this picture of steady progress.

When it colonized some temperate regions, *R. norvegicus* ousted a congener, *Rattus rattus*. This, colloquially called the black, house, ship or alexandrine rat, varies greatly in color (plates 2, 16, 18): in warm countries, where it often lives in the open, it is commonly tawny; the black variety is frequent only in temperate climates, where most of the rats of this species live in buildings. The color varieties are not sub-species, and should not be given sub-specific names: two or more may occur in a single litter [148, 724]. There are many closely related species in tropical countries [585].

Figure 1. *Rattus norvegicus.* An adult male on the run.

If they are regularly handled from an early age, individuals of both species can be tamed [47]; but there are no laboratory strains of *R. rattus. R. norvegicus* is a burrowing animal (figure 2) but it can climb and swim well; it lives readily in hedgerows, earth banks, hay ricks, and the ground near sewers and streams, as well as a variety of urban environments, including sewers. *R. rattus* does not often burrow or swim, but it climbs even better and typically nests above ground. In ports, such as London, both species sometimes live in the same building, *norvegicus* in the basement and *rattus* in the attics. *R. rattus* is often called the roof rat: it is exceedingly common in the village roofs and coconut groves of tropical countries. In temperate regions, including most of Europe, *rattus* is now almost wholly in the ports; in hot countries the same is true of *norvegicus.*

Both species have a long history of dependence on man, well described by Barrett-Hamilton & Hinton [67]. Living in human communities, and competing with man for food, may have led, by natural selection, to genetically determined changes in behavior; this applies especially to the avoidance of unfamiliar objects (such as traps) displayed by both species. The omnivory which they display may, however, have evolved before human communities became prosperous enough to support populations of small rodents.

The vast genus *Rattus* includes a few other species dependent on man. Some are of great economic importance: the "little" or Polynesian rat, *R. exulans,* small enough to nest in bamboo furniture, covers southeast Asia and the Pacific islands; like its larger and more notorious congeners, it can thrive both in buildings and out of doors. Most species are independent of human food production, but some are beginning to attract experimental scrutiny. The long-haired rat, *R. villosissimus* (plate 3), an inhabitant of the inhospitable arid zones of central Australia, occasionally breaks through its usual

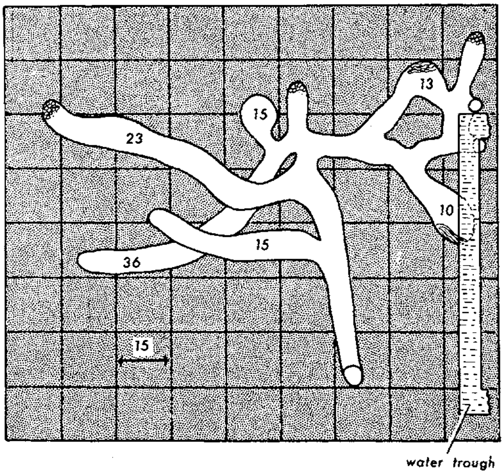


Figure 2. System of earth burrows of *Rattus norvegicus.* Figures show depths in mm. (After Pisano & Storer [525].)

ecological restraints and appears in enormous plagues. Despite its special habitat, its social behavior resembles that of the commensal species [54]. In general, so far as knowledge goes, the members of the genus are similar both in their repertoire of social signals and also in a high degree of behavioral adaptability, especially in their food habits.

Versatility is indeed a mark of the whole family of rats and mice, the Muridae, outstandingly so of its most numerous species, the house mouse, *Mus musculus*; in laboratories its many domestic varieties, with those of *R. norvegicus*, share with man the anomalous distinction of being the experimenter's most used guinea pig. It provides the best examples of experiments on some aspects of behavior, and appears in several places in this book.

Of the larger members of the family (outside *Rattus*), one, the Indian mole or bandicoot rat, *Bandicota bengalensis* (plate 4), resembles, in its own geographical region, *R. norvegicus* both in scope and in economic importance; in certain cities, notably Calcutta and Bombay, it seems largely to have replaced *norvegicus* [637]. There has, however, been surprisingly little research on its behavior; and the same applies to other, less notable murids. The concepts and methods described in this book, though based mainly on the study of one species, can be applied to the investigation of these others. Such work has begun, notably on the genus *Peromyscus* [369], and promises to give soon a new dimension to our understanding of mammalian behavior.

1.2 LABORATORY RATS

Most scientific studies of rat behavior have been on domestic varieties of *Rattus norvegicus.* All laboratory rats are of this species. They can easily be crossed with wild ones, but their behavior differs from that of wild rats in many important respects, not all of them obvious [42]. They have been selected for tameness, that is, for a reduced tendency to flee from man or to struggle or bite when handled. In addition, strange objects which would induce avoidance ("fear") by wild rats provoke mainly approach ("curiosity") by tame ones; and tame males do not attack other males with anything like the same intensity as wild males. Their selection of foods, when they are faced with a choice, may also differ from that of wild rats. A *similarity* of behavior, which they are rarely allowed to display, is that they burrow readily.

Differences in behavior have been paralleled by changes in growth, described by Donaldson [206]. There are also differences in the relative weights of organs, such as the adrenal glands. A population of wild rats is genetically heterogeneous, and generalizations about the behavior of wild rats often have to be qualified by reference to individual variation. In an inbred strain genetical variation is greatly reduced. This has the advantage, for certain kinds of experiment, that differences between experimental and control groups are more likely to be the effects of the experimental procedure, and less likely to be due to genotypic variation with which the experimenter is usually not concerned. Nevertheless, it is misleading to speak of "the laboratory rat" as if laboratory rats were quite uniform. First, some genetical variation always remains. Second, in inbred strains, minor differences of environment can produce marked phenotypic variation: in this respect, highly inbred animals may be less convenient material for experiments than the first-generation hybrids between inbred strains; such hybrids are both genetically *and phenotypically* often remarkably uniform. Their use may make possible a reduction in the number of experimental animals needed to give conclusive results [410]. Third, there are several varieties of tame rats in common use: in addition to the familiar albinos, which have pink eyes and poor eyesight, there are colored types—hooded, piebald, gray, and black—which have a pigmented iris and correspondingly better vision [317].

The existence of tame strains of a species which is also easily available in the wild form makes *Rattus norvegicus* a convenient animal in which to study behavior. But convenience has its dangers: a concentration of research on one species could lead to an absurdly incomplete and distorted picture of mammalian behavior. Accordingly, in this book, mention is made of other species wherever it seems important to emphasize resemblances to rats or differences from them; or when some aspect of behavior has been insufficiently studied in rats.

1.3 EXPLAINING BEHAVIOR

By behavior is meant here the whole of the activities of an animal's effector organs—its muscles and glands. The definition includes the contraction of smooth muscle and the secretions of all glands, but most of this book is concerned with behavior in a narrower sense, namely, the movements of the whole animal which depend on the activity of many skeletal muscles.

The account of behavior in this book is wholly in terms of overt activities which can be directly observed, and of physiology which can be studied by well-established laboratory methods. No reference is made to the feelings of rats, their thoughts, their minds, or any of a number of such concepts colloquially used in speaking of human behavior. This restriction is usual (though not universal) in scientific communication, and we may now inquire whether it is necessary. Most people seeing a rat sniffing around near food find it both convenient and sensible to say that the rat is hungry and looking for food; and, if the animal is then disturbed and runs away, to say that it has been frightened.

It is difficult to speak objectively about behavior because we attribute our own awareness, feelings, and thoughts, not only to other people (as, with due caution, we must), but also to other species. This anthropomorphism can lead to error in quite simple ways. For example, like most mammals, rats are greatly influenced by odors. A male can distinguish the odor of a female in estrus from that of a non-receptive female (§ 6.1.2). An unwary human observer, incapable of this olfactory achievement, might attribute the movement of a male toward a female out of sight or hearing to some mysterious and indefinable agency—perhaps called an "instinct"—beyond ordinary understanding. Rats also make and hear sounds of too high pitch for our ears (§ 5.2.4). These are examples of the different sensory abilities of different species: the "world" of sense impressions of an animal much influenced by smell, and responsive to sounds of high pitch, is quite different from that of one relying primarily on vision.

Another example is the attribution of a high degree of intelligence to rats. Wild rats are difficult to kill because they avoid traps and poison baits. They consequently often appear intelligent, and one biologist has been led to call the conflict between rats and men "a veritable battle of wits"; but careful observation of rats in simple experimental situations has shown that the avoidance of strange things is quite indiscriminate: it extends to harmless objects and even to wholesome food, and so is "automatic" rather than "intelligent" (§ 3.3). Of course, it greatly benefits the animals that display it.

Comparisons with human behavior can have their uses. Indeed, our tendency to *compare* other species with ourselves is not only "natural"; it is inevitable. It leads to error when it is assumed, perhaps unconsciously, that other species resemble us in matters in which, in fact, they differ from us profoundly. Comparisons must be made; but the *assumption of similarity* must be avoided.

The dangers of assuming similarity, that is, of arguing by *analogy*, are well known in physiology. A cavy, *Cavia*, deprived of ascorbic acid develops scurvy. To assume, by analogy, that rats without ascorbic acid would also become scorbutic would be logically unjustified; and in fact rats do not need this vitamin in their food. Yet analogies are universally popular. What role may they be permitted in scientific communication? First, they may be used in description. Anatomy has many examples, such as cloaca, cortex and labium. In ethology we may refer to certain movements of a fish or a bee as dances, and to the signals of mating rats as courtship; but we should be led sadly astray if we assumed that we could regulate the dances of other species by playing waltzes or reels. A second rôle of analogy is, however, legitimate—namely, to suggest testable hypotheses. We may observe a similarity, perhaps superficial, and test by experiment how far the similarity extends. Atz has discussed this subject more fully [29].

Whatever our method of speaking about behavior, a first objective in a scientific study is to describe it accurately and in some detail. This is far from easy. Secondly, we have to explain it. The two processes are in practice not separate.

In biology, two main sorts of explanation are used. First, any feature—structural, chemical or behavioral—of any species may be interpreted in terms of its *survival value.* For instance, an adult male wild rat in its territory threatens strange males of its own species. If one asks why it does so, the answer may be that the process of natural selection has favored a genotype which brings about this type of behavior. It may be said, or hypothesized, that such territorial behavior has a favorable effect on the structure of rat populations, and so confers a selective advantage on those that display it; this advantage could be due to the dispersal of rats sensitive in access to new sources of food. The causes of the behavior, implied in this statement, are events in the remote past which have acted in the first place on ancestors of the animals observed. An objection is that this kind of explanation cannot be tested: we cannot return and investigate the operations of natural selection in an earlier epoch. It is, indeed, often difficult to demonstrate experimentally the survival value of behavioral features as we observe them today, though this sort of question is open to systematic investigation.

Accordingly, in this book, explanations are principally of a second type. The behavior of, say, an adult male rat may be explained in terms of events which influence it directly, either at the time of the activity in question or at least during its own life history. This kind of explanation has several subdivisions. (i) Behavior is influenced by external stimuli. (a) These may produce an effect at once, as when the sight and odor of another male leads to attack. Or (b) the past experience of successful encounters with other males may help to induce the male to attack again: this is an example of the effects of external stimuli which have acted earlier in the life of the animal. (ii) Behavior is also influenced by internal states, such as the amount of male hormone in the blood; a young male does not threaten strange males until its testes begin to secrete this hormone at a certain rate. Of these two kinds of explanation, type (i) may be said to be behavioral, type (ii) physiological. None of these sorts of explanation is incompatible with any other, nor can one replace another. Often, one method of analysis suggests problems which have to be solved by another method, as when observation of behavior leads to a study of endocrine organs.

All explanatory propositions of the second type have an important logical property in common: if sufficiently clearly stated, they are capable of being falsified; we can imagine observations which would disprove them. They therefore qualify as scientific in the most rigorous sense of that term.

Given these kinds of explanation, we may ask by what criteria we judge an explanation to be valid or acceptable. In practice, two tests are commonly applied. A particular observation, or group of observations, may be put in a larger class of phenomena or, more generally, may be incorporated in some accepted frame of reference sometimes called a paradigm. If it is asked why male wild rats attack other males, the reply may be that territorial behavior is common among the vertebrates, and this is an example. Such a statement can be at least moderately satisfying: it relates the conduct of male rats to the general proposition that behavior patterns are usually advantageous (owing to the operation of natural selection); it also relates the fighting of males to the general notion of territorial behavior.

The second test is more stringent: an explanation should make possible correct *predictions*; that is, an explanation is said to be valid when it is a general statement from which it is possible to deduce particulars. The statement that all adult male wild rats attack strange males is of this kind, though it is not one of very high generality (nor is it quite true). Another example is: territorial behavior by male mammals depends on the presence of male hormone in the blood. Both are readily tested by experiment; if the results of experiments conform with the proposition tested, then it is held to be to that extent valid.

There is a further distinction. It is often felt that physiological explanations are superior to others. This is an inappropriate way of expressing a real difference. A physiological account of behavior has two special features. First, it gives the immediate causes of the behavior, both external and internal; it should therefore enable us to change the behavior more easily, more extensively and more certainly than before. Secondly, it relates the internal organization of the animal to its behavior; this should enable us to predict the way in which the animal will behave from knowledge of its organization. We are, however, a very long way from any substantial achievement on these lines.

2 Brain and Behavior

When all is said and done, the fact remains that, for the beginner, the understanding of the brain's structure is not an easy thing. It must be gone over and forgotten and learned again many times before it is definitely assimilated by the mind. But patience and repetition, here as elsewhere, will bear their perfect fruit.

William James

2.1 THE ROLE OF THE BRAIN

Of all physiological facts, those concerning the brain seem most likely to help to explain behavior; and, although this statement is a truism, we may now ask why it is so. The answer given in this chapter inevitably refers to kinds of behavior, and experimental methods, that are more fully described later. Hence some readers may find it convenient to return to this chapter after they have read further. The central nervous system is the organ through which the sense organs act on the effectors: although all other organs may influence behavior, the CNS and the nerves carry especially large amounts of information to the muscles and glands. While the blood enables the muscles to remain operational, by carrying substances to and from them, the nervous system determines the moment, duration and intensity of the contractions of each muscle and also their relations to the contractions of other muscles.

Neural action, then, imposes a *pattern* of activity on dozens of muscles and many millions of muscle fibers. Patterning exists even in a simple reflex. C. S. Sherrington (1859–1952) wrote: "A great principle in the plan of the nervous system is that an effector shall be at the behest of many receptors, and that one receptor shall be able to employ many effectors" [606]. This arrangement makes possible the interaction of many afferent inputs to produce the animal's pattern of activity. There are also patterned activities within the CNS that influence behavior. These have been called, by J. Z. Young, representations of the external world of the animal [729]. They may be characteristic of the species, in which case the behavior they determine is of the kind called "stereotyped" in this book. Or they may be the result of the adaptation of the individual to its own particular environment; they are then the result of the storage of information in the brain during the individual's own lifetime. Altered behavior of this sort is an example of individual or physiological adaptation. It differs from genetical or phylogenetic adaptation, in which the genotypic make-up of a population is changed. All animals display physiological adaptation: an organ which is subject to much use, instead of wearing out like a part of a machine, often enlarges or becomes more efficient in some other way.

We can talk of "representations" only vaguely, because we do not know how information is stored in the nervous system. But we can be more precise about the input to which the brain is continually responding in the awakened animal. Information is unceasingly fed into the brain from the external sense organs which give a picture of the outside world, and also from the internal sense organs which give a picture of the state of the body from moment to moment. The proprioceptors make a large contribution: almost half the axons of the nerve which supplies a skeletal muscle are sensory, and most of these are proprioceptive; that is, they register deformations and stresses in the moving parts (muscles, tendons and joints) [416]. Injury to the tracts of proprioceptive fibers destroys the fine pattern of movements.

In performing its many functions the CNS is very unlike most machines. Consider the recognition of shape. If one wished to devise a machine which responded in different ways to a number of different shapes, one would first think, perhaps, of an array of photoelectric cells, as a parallel to the light-sensitive cells of a retina, linked to a computer, or "brain"; but as soon as we consider what a retina and brain actually achieve, such crude comparisons fail. First, recognition by an animal such as a rat [307] or an octopus [730] does not depend on the position of the image in the visual field; provided the receptors are activated in a specific pattern it does not matter which receptors are in use. Secondly, the size of the object relative to the visual field, and the angle at which it is presented, can vary over a wide range; this is stimulus generalization. To devise a machine even with only these properties is a formidable task, though, as Casey & Nagy have described, something of the sort is now being attempted [147]. Finally, as we see below, removal of a substantial part of the region of a rat's brain (the striate cortex) especially concerned with vision does not always destroy these abilities.

2.2 METHODS OF STUDY

2.2.1 Structure

A first step toward understanding is to study structure, both gross and microscopic, in a given species or, better, in a series of species. The brain of a rat is illustrated in figure 3. It is typical of a small mammal.

The brain stem (medulla, pons and midbrain) is, like the spinal cord, largely an assembly of reflex centers: it receives the inputs of the cranial nerves, except the olfactory and most of the optic, and contains the origins of the motor fibers in them. Particular regions are associated with specific reflex acts such as lachrymation, with more complex patterns such as breathing and (in the midbrain) with postural adjustments. There is also a large cerebellum of which the function is evidently the control of the details of movements: it is the cerebellum which (as far as we know) makes the proprioceptive feedback effective. In all this the mammalian brain resembles that of other classes of vertebrates.

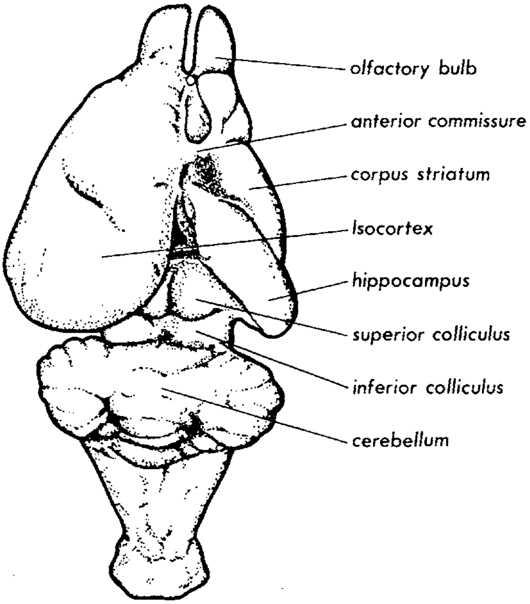


Figure 3. Brain of rat: dorsal view with dorsal cortex and corpus callosum removed on right. (After Beach [72].)

The most distinctive feature of the mammalian CNS is the increase in relative size and elaboration of the forebrain. The only part of the forebrain which largely retains its primitive role is the hypothalamus. It is usual to emphasize the vastly enlarged cerebral hemispheres (figure 4) which have an outer layer of cellular tissue, the cerebral cortex. Most other vertebrates retain the nerve cell bodies within the tracts of fibers (white matter) which connect one part of the CNS with another. The working of the cortex, however, cannot properly be discussed without reference also to the thalamus, which too, in a mammal, is especially large and complex: most of the afferent pathways to the cortex pass through the thalamus; from there impulses are relayed to the cortex (figure 12). Thus the cortex has converging upon it the main input from the special senses. Also large and complex—though until recently they have received less attention—are structures at the base of the forebrain now often called, with parts of the cortex, the limbic system (figure 9). The cerebral cortex, the thalamus, the limbic system and the reticular activating system are certainly all in continuous interaction; no one can be understood without the others.

The enlargement of the forebrain has been accompanied by changes in its functions. The forebrain originated as an olfactory receiving station; but during the rise of the mammals, and also on a number of lines of evolution within them, the olfactory influence has diminished. Part of the forebrain of all mammals has a specific motor function: the output to the skeletal muscles originates in a particular part of the cerebral cortex (in man, the pre-central gyrus); the pyramidal tracts run from here, to make (in many mammals) direct synaptic connection with the motor neurons of the ventral horns of the spinal cord; from the latter pass the fibers which end in the motor end-plates of the muscles themselves. There is consequently a unified and direct control of behavior by the cortex and its associated structures.

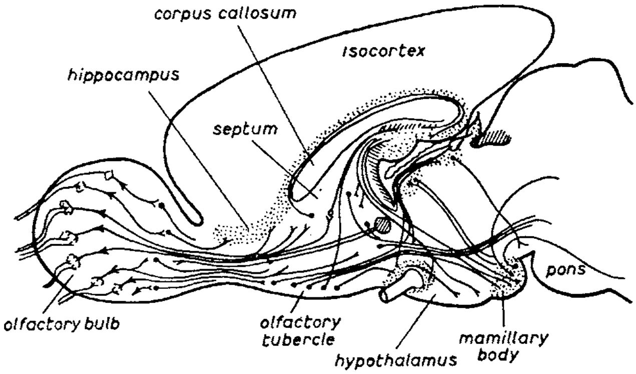


Figure 4. Olfactory and related connections in the rat brain (After C. J. Herrick [318].)

Within the mammals the complexity of adaptive behavior can be related to brain size, though not in any simple way or large whales (Cetacea) would be five times as intelligent as man. As Anthony [21] has shown, the significant relationship is not even weight of brain in relation to body weight; if it were, marmosets (*Hapale*) would be more intelligent than any other Primates. The important properties, in relation to intelligence, are of a different kind. The most primitive of extant eutherian mammals, the Insectivora, have a forebrain still largely dominated by the olfactory input; most of the non-olfactory cortex receives afferents from the other exteroceptors. Much the same applies to the rodents (figure 4). The Primates, at the other end of the scale, have large cortical regions which are not directly related to any special sense; nor are they motor. The progressive reduction of olfactory influence on the cortex and the increase in non-specific areas are the main structural concomitants of behavioral complexity among mammals.

One other general, quantitative feature of the brain is obviously important: the numbers of cells in the forebrain, especially the cortex, are vast, and their connections are bewilderingly elaborate. Each neuron is in synaptic connection with hundreds of others; and there are arrangements between the cells of different cortical layers which resemble the feedback loops of engineers.

2.2.2 Injury and Localization

The study of structure, gross or microscopic, gives only the beginnings of knowledge of brain function. R. L. Gregory has compared the pictures of connections in the CNS derived in this way to the blueprints used by engineers: they provide a lay-out of the components, but no information on their functions. It is (he adds) possible to say something of the impulses which pass in the tracts of nerve fibers, and of the results of interrupting them. Such accounts of the brain may be compared to wiring diagrams: they do not say what the parts do, only how they are connected [in 677].

Since clinical information was available before the results of experiments, early notions on localized function in the brain came largely from study of the effects of injury. This is like trying to find out how a very complicated and delicate machine works by taking a hammer to bits of it at random. The method, together with some more refined procedures, has, however, yielded the familiar maps of the cerebral cortex (figures 5 and 6). The maps show the main projection areas and the motor area. There also exist, for some species, quite detailed maps of the somatic sensory region, in which the surface of the body is represented in a distorted form corresponding to the relative importance, as sources of information, of the districts of the skin: the snout of a pig and the fingertips of a man have enormous representations. The main motor area, too, has been mapped; here the representation of the somatic musculature reflects the complexity of the movements performed: muscles of the human larynx and fingers have especially large regions. All such maps are now regarded as showing the points of arrival and departure of the main, specific afferent and efferent tracts; they tell us little about what the cortical neurons, in all their variety, are doing.

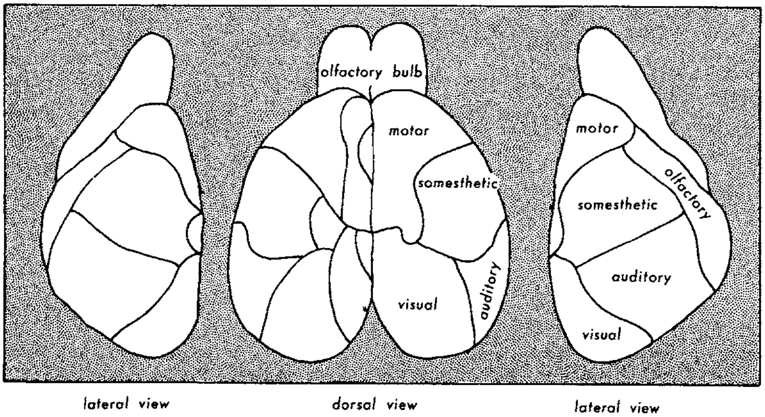


Figure 5. Brain of rat: the maps show histologically different areas and the supposed "functions" of some of these areas. (After Lashley [393].)

Behavior after brain injury has been studied in rigorous conditions in the laboratory, where it has often led to valuable observations. Most of the experiments involve making roughly symmetrical bilateral lesions in the brains of rats, cats or monkeys. Some examples are given later, in this and other chapters. The results are far from easy to interpret. One formidable difficulty arises from certain special properties of nerve tissue. If skin, muscle, bone, liver, kidney or other tissues are seriously damaged, the loss can be restored by compensatory growth; cells, previously quiescent, enlarge and may even divide. But the quota of neurons of an adult is fixed early in life; if some are later destroyed, they are not replaced. The only compensatory growth displayed by nerve cells is in their processes, especially their axons, which grow again if cut. From this we might suppose the effects of injury to be irrevocable. Yet in fact, an animal (or man) seriously handicapped by brain damage may undergo a gradual, and sometimes astonishingly complete, recovery of function.

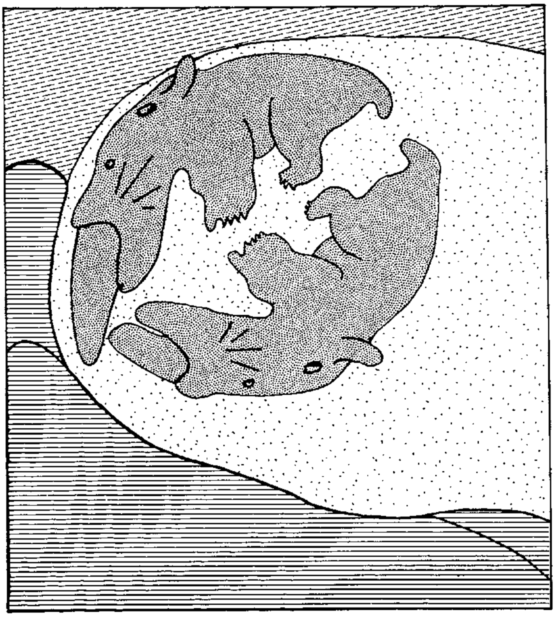


Figure 6. Sensory and motor localization in the cerebral cortex of the rat. On the left the pattern of representation of motor function in the pre-central area: on the right, the sensory map—an approximate mirror image of the motor. (After Woolsey [723].)

The physiology of this recovery is quite unknown. Its occurrence warns us, however, not to take it for granted that the brain is divided structurally into parts with individual functions. If we require an analogy from the physical sciences, we may turn to optical holograms: these are systems which, like an ordinary photograph, record the appearance of an object or scene; but any portion of a hologram, above a very small minimum size, allows reconstruction of the *whole* of the image recorded. A related enigma concerns a major structural feature of the brain which, though obvious, is sometimes ignored. Nearly every part of the brain is represented twice, once on each side. When the effects of small experimental injuries are studied, the lesions are usually made as symmetrically as possible on both sides: unilateral injury often has little detectable effect. In most experiments, the bilateral lesions are made during one operation, but in a few the injuries have been inflicted in two stages. Stein and his colleagues destroyed substantial regions of the frontal cortex or of other parts of the cerebrum of rats. When this damage was done in one stage, the rats took many more trials to learn simple tasks than did control rats which had been given only sham operations with no brain injury. But when the injuries on the two sides were made at an interval of thirty days, the performance of the experimental rats was no worse than that of the controls [644]. The uninjured tissue must be involved in some process, as yet obscure, which compensates for the initial damage.

2.2.3 Electrical and Chemical Methods

Probably, advances at the cellular level will be needed for major progress in understanding the brain. The great achievements of cellular neurophysiology so far have been in the analysis of the nerve impulse, that is, the electrical and chemical changes in axons and at synapses. This work has been largely on peripheral nerves and autonomic ganglia, but is now being extended to cover what happens in the brain, as we see below. Synaptic connections become more efficient with use (at least in the spinal cord), perhaps as a result of the swelling of dendritic buttons or processes [212, 728]. Such improved connections must involve both excitatory and inhibitory synapses. Certainly, all behavior involves, not only excitation and inhibition as these terms are used in describing behavior, but also the excitation and inhibition of neurons. This balance between two opposite effects in the CNS is now, as far as the reflex activity of the spinal cord is concerned, a part of classical physiology: a spinal reflex requires the firing of inhibitory impulses which reduce the contractions of the muscles antagonistic to those producing the reflex movement. Something is even known of the physical basis of inhibition: just as the firing of a neuron by the arrival of impulses involves the depolarization of its membrane, so inhibition probably depends on hyperpolarization [212].

The character of the problems presented by the brain is illustrated by an electrical technique that has been used to study the cortex. This is strychnine neuronography. Small fragments of filter paper, soaked in a solution of strychnine, are applied to points on the cortex in a living animal. The strychnine causes synchronized discharge of the neurons it affects, and the synchrony appears wherever the axons of the strychninized cell bodies are distributed; in all such areas a cathode-ray oscillograph can pick up a so-called strychnine spike. The application of this method to the visual areas of the cortex has been reviewed by Hebb [307]. Brodmann's areas 17, 18 and 19, which are structural divisions of the primate visual cortex in the occipital region, have major connections with the separate areas 8 and 20. The two areas 17 (left and right) receive the optic input from the thalamus, and there is a point-by-point representation of the two retinae in them. Strychninization shows that fibers pass from 17 to 18, but in a diffuse manner: local excitation of 17 is conducted to a large part of 18, and thus topological reproduction of retinal activity breaks down.

Excitation of any part of area 18 is conducted to all other parts of area 18, to the nearest part of area 17, and to all parts of areas 19 and 20. Moreover, there is convergence as well as spread of excitation: for example, cells in different parts of 18 may have connections with the same points in 20. The classical "reflex-arc" kind of picture of central nervous function clearly will not do for a system arranged like this.

The visual system has been further illuminated by the celebrated work of Hubel & Wiesel. They used a delicate method of recording electrical changes in neurons by means of microelectrodes. They stimulated very small regions of the cat retina, and observed the resulting discharges by individual neurons in the primary visual cortex, or striate area. Some neurons respond to the onset or offset of light in a narrow, elongated region; around this region, stimulation has the opposite effect: hence these neurons respond especially to edges. Other neurons in the striate cortex have larger receptive fields. As we saw above, the primary visual projection area itself projects into secondary visual areas of the cortex. In these, Hubel & Wiesel found neurons which discharge most in response to more specific features of shapes, such as the particular orientation of rectangles [335].

Other studies of the electrical activity of the brain have been less successful. We know from the extensive use of the electroencephalogram (EEG) that, when a subject is resting, the brain, or at least the cerebrum, maintains regular changes in electrical potential that can be picked up by electrodes fastened to the scalp. The changes revealed by the EEG are evidently general in the mammals; Bergen [85a] has studied them in the rat. It is, however, not known how the various rhythms of electrical change are maintained or what functions they serve.

2.3 ISOCORTEX AND THALAMUS

2.3.1 The Main Structures

The cerebral hemisphere of a mammal consists of a phylogenetically ancient part which is medial and ventral, and a new part which is much the larger and has until recently been much more studied. The terminology of these structures is confused. Here, that of Pribram [in 291] is used: the more recently evolved dorsolateral cortex is called the *isocortex*, corresponding roughly to the neocortex or neopallium of comparative anatomy; it is distinguished histologically by having six layers of cells at some stage in development.

The isocortex may be subdivided according to the character of the thalamocortical tracts reaching it. The thalamic nuclei are of two kinds: (i) the extrinsic nuclei, which receive large afferent tracts from outside the brain; (ii) the intrinsic nuclei, which receive fibers mainly from other parts of the thalamus. Accordingly there is the extrinsic cortex, corresponding to what we have already called the primary projection areas; and the intrinsic cortex (equivalent to the "association" areas), of which the various regions receive fibers only from the intrinsic thalamus. This description ignores the motor cortex; but the latter does in fact receive extrinsic projections from the thalamus; further, the pyramidal (that is, cortico-spinal) tracts originate partly in regions of the cortex other than the primary motor area.

The thalamo-cortical tracts are paralleled by similarly vast projections in the opposite direction. Large cortico-thalamic connections provide a means by which excitation can pass back to the thalamus as well as from it. Hence there is a structural basis for continual interaction between telencephalon and diencephalon.

2.3.2 Habit Formation and Localization

An outstanding example of an attempt to relate brain function to behavior was that of K. S. Lashley (1890–1958). The animals he principally used were laboratory rats, but he also worked on monkeys. The behavior studied was the learning of discriminations and simple manipulations, and how to find the way through a maze of branching passages. His method was usually to destroy portions of the isocortex, or to make cuts in it, with an electrocautery, and to study the effects on behavior. Lashley himself published a late review of his work in 1950 [394]; other valuable discussions are those of Osgood [514] and Zangwill [in 677]; but Lashley's own earlier work should be consulted for its historical importance and the elegance and interest of the writing [76, 391].

Lashley's most remarkable experiments are those which suggest (i) that learning any task, regardless of its nature and the senses involved, is a function of the whole cortex; (ii) that the ability both to develop new habits and to retain old skills is proportional to the *amount*, regardless of region, of cortical tissue present ("mass action"); and (iii) that one part of the cortex can take over the functions of others that have been destroyed ("equipotentiality").

One of the concepts strongly criticized by Lashley was that of the reflex arc, with its overtones of a telephone system, as applied to the brain. He made incisions between the visual and motor areas of the cortex of adult rats. He then trained them to make a difficult discrimination: this involved their avoiding X and approaching △ when these were presented on a black background, but approaching X and avoiding △ on a striped background. For this he used the arrangement shown in figure 7. This seemed to dispose of any simple sensori-motor connections as the basis of learning; but since this work was done, the extent of the connections of the cortex with the thalamus and reticular formation have come to be more fully understood; and these connections were left intact in the experiments.

More important work involved the destruction of parts of the cortex. Rats were operated on and tested for maze-learning ability. Three mazes were used, with one, three or eight blind alleys. The decrement in learning ability was proportional to the *amount* of cortex lost, regardless of the locus of the damage. Rats which had learned to run mazes before operation were tested for retention of the habit: retention too was found to be proportional to the amount of tissue remaining. Comparable observations were made on rats which had to learn to release themselves from a box by depressing a platform. In habit formation of this sort, however, the injured animals sometimes averaged better than the controls: the latter tended to be too active. In this, as in other instances, much depends on the character of the problem.

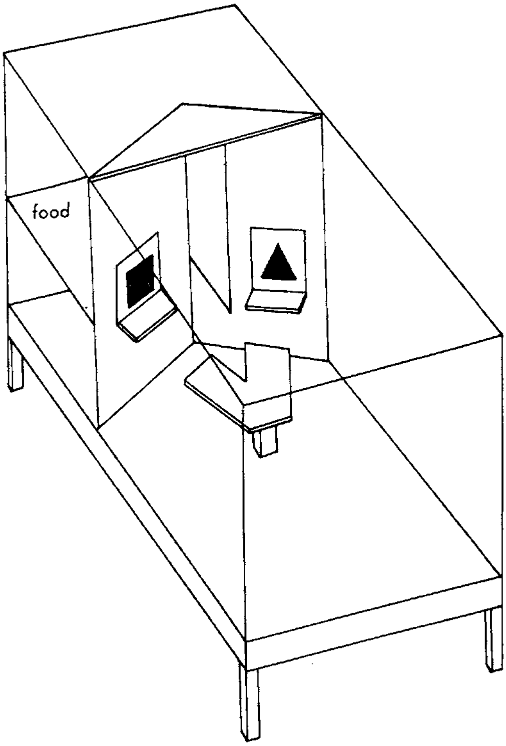


Figure 7. Equipment for studying visual discrimination. Of the two doors marked with different patterns, one is unlocked and gives access to food when a rat jumps at it. (After Lashley [392].)

These observations seemed to contradict well-established facts of cortical localization. Yet some other results went further, since they suggested that the primary projection areas play a part in habit formation even when the sense organs which supply the input to them have been destroyed. Rats were blinded and required to learn a maze. The visual cortex was then injured; as before, the loss of habit was proportional to the extent of the damage. Later Tsang reported that rats blind from birth were similarly affected by injury to the visual cortex [686], and this has been confirmed by Lansdell [387]. The work of Lashley and of Tsang has been criticized, notably by Finley, on the grounds that the lesions may have extended beyond the visual region [236]; but subsequent experiments by Lashley went some way to meeting Finley's objections.

Other work by Lashley, on visual discrimination, leaves a more confused picture. He first produced evidence that rats' learned responses to different degrees of brightness are impaired by lesions in the occipital third of the cerebral hemispheres; and that the extent of the lesion, us usual, determines the degree of the loss. Later, however, he identified a small region of the visual cortex which is crucial for the acquisition and retention of visual discriminations: injury to this fragment of tissue, evidently, determines the decrement. This does not fit the notions of mass action and equipotentiality.

Other observations, too, conflict with an unadorned mass-action hypothesis. Lansdell studied the effects of brain damage on habit formation by rats which had been regularly handled and had been reared in a complex environment: these animals were more "intelligent" than rats kept in the usual small cages. (They were tested by the Hebb-Williams method, described in § 7.3.4.1 and figure 63.) Lesions in the front part of the cerebral hemispheres had no effect on performance. Lansdell comments that this region of the rat or the human brain is evidently not important in the solving of simple, familiar problems [387].

All these observations concern rats. Other work has been principally on Primates. Here the evidence for localization is stronger, that for mass action, weaker [677]. This applies to the vast but unsystematic information we have on the human brain, but also to the results of laboratory experiments on monkeys (particularly *Macaca*) and on chimpanzees (*Pan*) [248].

The findings on the immediate effects of cortical injury need to be integrated with those on recovery of function after damage. Dawson, in a critical review, shows that more information is needed on the precise character of the lesions inflicted by experimenters. Moreover, although there is no hyperplasia after destruction of neurons, there may be growth or regrowth of the processes of nerve cells. The rôle of this process remains an enigma [188].

2.3.3 Studies of Responsiveness

The isocortex is usually thought of as a vast organ of "learning"; but in fact it also influences both the variability of behavior and the intensity with which fixed patterns of behavior are performed.

Krechevsky studied the effects of isocortical damage on exploration by rats. Rats tend to vary their route to a goal when there are alternative paths of similar length. This variation was reduced by the lesions; the reduction was proportional to the extent, and independent of the locus, of the injury. In other experiments rats with damaged brains chose a stereotyped path to a goal, whereas intact rats preferred a route which was varied by the experimenter [382]. In these experiments a damaged cortex led, then, to perseveration of a habit, and therefore to a loss of behavioral adaptability.

Beach has made analogous observations on reproductive behavior. The maternal activities of rats after cortical lesions were impaired in proportion to the size of the injury. There was also a positive correlation between the amount of cortical tissue remaining and the proportion of males still able to copulate (figure 8). A curious feature was that the deficits could be made up by injecting the appropriate hormone [71, 74].

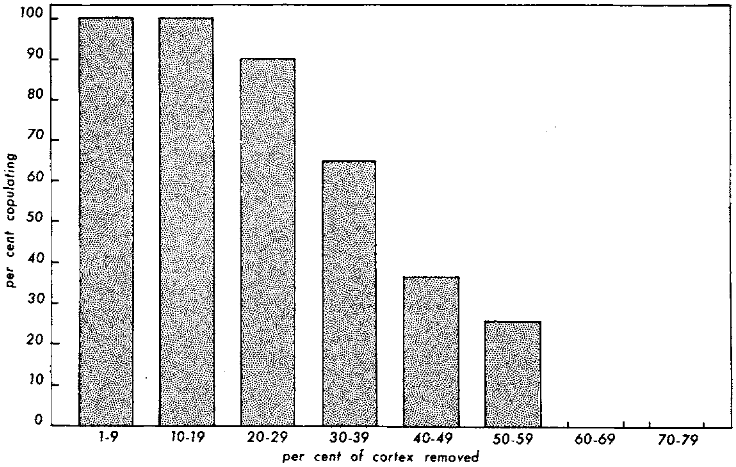


Figure 8. Effect of cortical destruction on mating behavior. The percentage of male rats copulating after cortical injury is proportional to the amount of cortex that remained. (From Beach [71].)

Much of the work cited in this and the preceding section suggests that trial-and-error behavior, exploration and also fixed action patterns depend in certain respects on a general action of the whole of the isocortex, at least in so lowly a mammal as the rat. The contradiction of the facts of localization may be only apparent: regions of the cortex which have specialized functions may have a "mass" function as well; perhaps there is, as Lashley suggested, a general facilitatory influence of all regions. In more complex brains, especially those of the Primates, the cortex evidently becomes more differentiated; but even in them there may be some mass action, perhaps especially during early life.

2.4 THE LIMBIC SYSTEM

The remainder of the cortex, together with certain associated structures, is sometimes said to consist of centers of the "emotions" or sources of "drive"; but these terms are ambiguous or vague. For comparative anatomists this system consists mainly of the phylogenetically ancient archicortex and palaeocortex. Here they are called the limbic system (figure 9). The system includes (a) the receiving centers of the olfactory input and (b) a number of other structures with no special association with the olfactory sense. They form a unit only anatomically, and the knowledge we have of their functions has been described as contradictory and bewildering.

The fibers from the olfactory organs first make synaptic contact in the olfactory bulb (figure 4). Of the neurons in the bulb, the mitral cells send afferents to the pyriform lobe (paleocortex) which forms the lower lateral part of each hemisphere; from there further fibers pass to other cortical structures. Bilateral injury to the pyriform lobe may lead to loss of acquired responses to odors. Other (tufted) cells of the olfactory bulb send afferents to

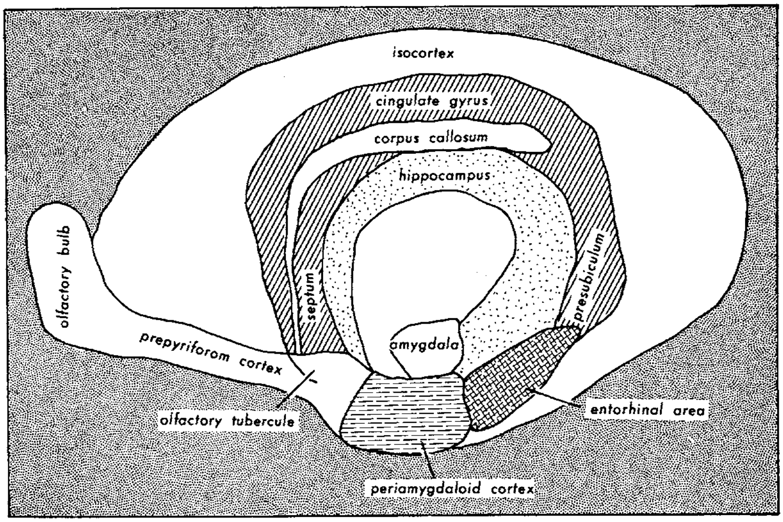


Figure 9. Diagram of sagittal section of rat brain to show the main components of the limbic system.

the amygdalae in the floor of the forebrain. Electrical stimulation of the amygdalae and neighboring parts of the cortex (prepyriform) evokes actions used in eating, such as lip movements, sniffing, chewing and licking; salivation also occurs. Such findings suggest a purely relay function for the olfactory bulbs, but this is misleading. As we see later (§ 4.3.1.2), Hankins and others have brought evidence of an integrating function: the bulbs are evidently concerned not only with the olfactory input, but also with that from the taste organs [287]. The same applies to other parts of the limbic system which too have been supposed to be concerned with smelling. (The system used to be called the rhinencephalon.) Most of the limbic system of mammals, like the isocortex, is freed from attachment to any one sensory modality. Similarly none of the limbic regions is specifically related to particular motor functions. Electrical stimulation may alter processes which are regulated ordinarily by the autonomic nervous system (ANS), but in unpredictable ways: respiratory rate, blood pressure, salivation and gut peristalsis— among other processes— may be raised or diminished, and a slight shift in the position of the electrode may alter the response. Yet injuring parts of the limbic system leads to no detectable malfunction in these autonomic activities. Here is a sharp contrast with the effects of damage to the hypothalamus, as we see below.

Studies of these cortical structures have been reviewed by Brady [in 291]. He uses the terms "paleocortex" and "allocortex" synonymously: they refer only to structures which (i) "have a clear phylogenetic primacy" and (ii) meet the criteria for cortical regions of at least three layers, of which the superficial layer consists of fibers. This group includes only the hippocampus, the pyriform lobe and the olfactory bulb and tubercle. The term "juxtallocortex" is applied to cortical regions intermediate between the ancient allocortex and the young isocortex (neocortex): they include the cingulate gyrus and the presubiculum. A third group of structures are functionally (it seems) closely related to the first two, but do not meet the criteria for cortex: they include the amygdalae and the septal region, both of which seem to have intimate links with the hypothalamus.

Interference with these structures can drastically alter complex behavior. Again this has been shown largely by the effects of bilateral injuries, but partly by the results of local stimulation with implanted electrodes. Stamm, for instance, made small lesions in the cingulate cortex or the hippocampus of rats and so produced severe disturbances of maternal behavior, hoarding and other stereotyped activities [640]. As Peretz has shown, such injuries also influence habit formation: he too made lesions in the cingulate cortex of rats; one consequence was a slowing in the rate at which the animals learned to avoid a noxious stimulus [522]. The precise character of the defect induced by the lesions is often difficult to define. In this case, however, some advance has been made by Slotnick. He studied the maternal behavior of females with such lesions: the individual activities were duly carried out, but their *sequence* was disordered [614].

According to some findings, damage to parts of the system make the animal fiercer. A mammal with its whole forebrain destroyed can be kept alive for some time; such a "midbrain" animal is liable to display "sham rage"; that is, it makes responses normally evoked by a conspecific rival (see §§ 5.2, 5.3) in the absence of any appropriate stimulus. It is rather disconcerting that such behavior can be induced (in rats and other mammals) by injury to the olfactory part of the limbic system. Release of such "expression of the emotions" can also result from lesions in the cingulate gyrus or the amygdalae. Hence the juxtallocortex and associated structures seem to exert an inhibitory effect on the midbrain system responsible for sham rage. This notion is supported by some results of removing the whole neocortex in cats, but leaving the limbic system: the animals are notably placid and unresponsive to disturbing stimuli.

But other findings fail to fit the picture. Although, as we saw, injuries involving the amygdalae have led to increased responsiveness and sham rage, much work has been done with opposite results. In several species bilateral amygdalectomy has produced a taming effect. Some of the work on rats has been carried out in two stages. First, lesions were made in the septal region (figure 10); these led to wildness of behavior and also, sometimes, to loss of fear responses which had been induced by training before the operation. Second, in a few animals made fierce in this way, injury to the amygdaloid nuclei has resulted in taming.

The hippocampus, too, is evidently involved in violent responses, but its rôle is exceptionally obscure: its function has been said to change with each new experiment—a clear indication that the right questions have not yet been asked about it. It has been studied in some detail in cats and monkeys, and also in rats. Stimulation can be carried out with an electrode arranged so that the animal has freedom of movement. When the current is passed, the animal gives an impression of increased alertness or, sometimes, of more vigorous arousal expressed as "anxiety" or even rage. Similar effects are produced by the direct application of cholinergic drugs. In the rat, hippocampal lesions can lead to loss of responses learned before the operation. A curious observation made on the rabbit is that, when there is a fast electrical discharge in the isocortex, there is a slow one in the hippocampus, and conversely.

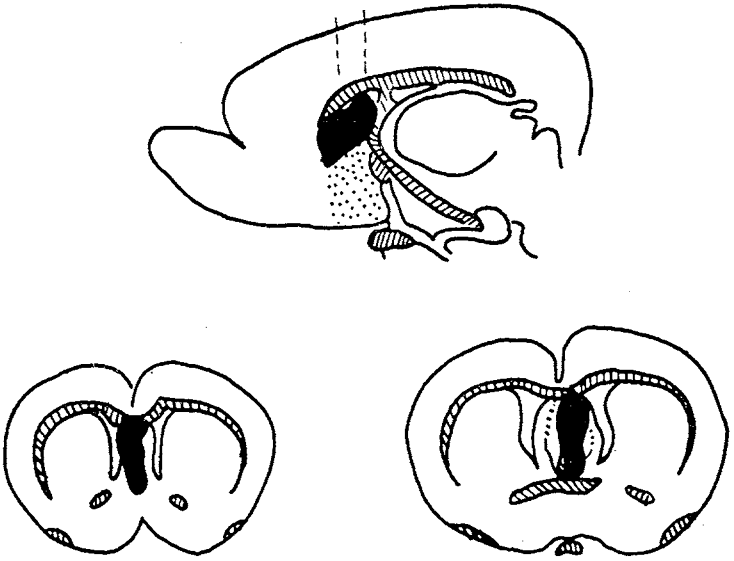


Figure 10. Septal lesions: above, sagittal section; below, two transverse sections. Lesions of this sort lead to wild behavior by previously tame rats. (After Brady [in 291].)

In 1954 the study of limbic structures was given a new dimension by remarkable experiments on the effects of self-stimulation of the brain. An electrode is implanted in the brain of a rat (or other mammal, such as a cat or a monkey), and is so connected that the animal can, by pressing a lever, pass a brief electrical charge through it. The wires which connect the electrode to the apparatus are flexible, and allow the animal to move about. To assess the effects of this stimulation, it is necessary to know at what rate the animal presses the lever when doing so has no effect. In typical experiments, unstimulated rats in these conditions spend 4 to 10 percent of their time pressing the lever (according to an arbitrary way of expressing the time spent on various activities). It might be expected that, when the current is switched on, the animal would be put to pain or discomfort; or, behaviorally, that it would quickly learn to avoid giving itself even these very mild electric shocks. This was indeed the finding of Delgado and his colleagues, in one of the two pioneering investigations: in some positions the electrodes give scores of from zero to one percent [192]; stimulation may then be said to have a punishing action. But Olds & Milner [511], the other pioneers of this method, found a rewarding effect. The program of research which arose from their work has been reviewed by Olds [510]. As figure 11 shows, rewarding are more numerous than punishing regions. When the electrode is in any of the former, the animal repeatedly stimulates itself: the stimulation may continue for hours at the rate of thirty responses every minute. The effects are usually observed when the electrode is in the limbic system, but also when the anterior part of the hypothalamus is involved. In a more usual type of experiment, an animal learns to press a lever when doing so releases food or water; and it learns to avoid the lever if pressing it produces an electric shock to the feet or a sharp puff of air. In the experiments on self-stimulation, it is as if the experimenter, in the placing of the electrode, is directly influencing the "mechanism" of rewarding or punishing effects in the brain. Correspondingly, rats will learn to find their way through a maze when the reward for doing so is the opportunity to perform self-stimulation.

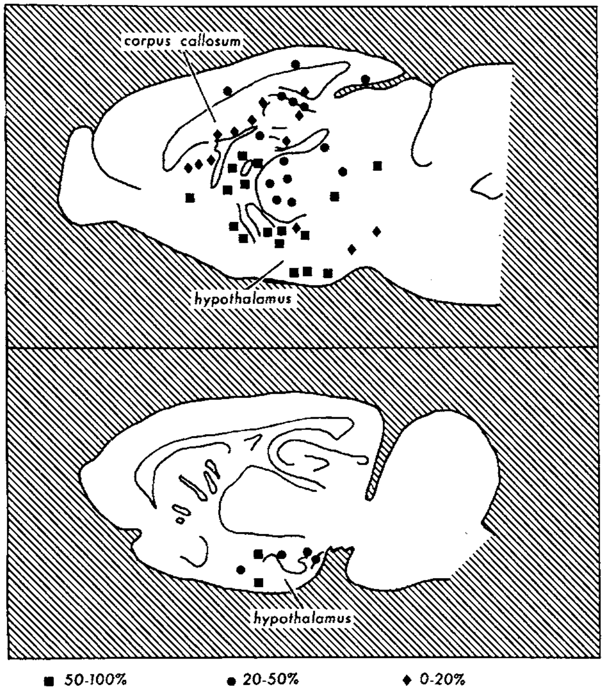


Figure 11. Sagittal sections of rat brain illustrating effects of self-stimulation by rats. Electrodes implanted at points shown by black squares were highly "rewarding"; black circles indicate moderate reward; and diamonds neutral or negative effects. (After Olds [508].)

Rats will, however, not only learn to turn the current on but, if the current then remains on, will learn the way to another point where it can be turned off. Perhaps it is the onset of the excitation that is sought. As a further complication, after long periods of self-stimulation rats become wild and savage; and in the intervals between such periods the animals behave in an agitated way.

The high self-stimulation scores may, as Olds [509] suggests, occur when the stimulus affects regions especially concerned with the satisfaction of homeostatic needs: normal stimulation of such areas would, perhaps, occur when such a need is met, and would lead to the ending of the activity provoked by the need. Such a system must of course be associated with the parts of the CNS which control overt behavior, since the latter too has to be adjusted to need.

2.5 THE RETICULAR SYSTEM

In most elementary accounts of the brain, the brain stem is described as an arrangement of well-defined reflex centers. The centers are highly specialized in function and can operate independently of the forebrain: a "midbrain animal" is one in which the forebrain has been destroyed; it still has an array of reflex responses. But paradoxically the midbrain also has a component of which the functions are generalized and not specific and which operates in intimate relation to the forebrain. This component, the reticular activating system (RAS), consists of large numbers of cells, most of them without long axons, whose functions were for long an enigma. In 1949 Moruzzi & Magoun published observations which have given the RAS a prominent position in neurophysiology. The subject has been reviewed by Jasper and colleagues [345] and by Magoun himself [424].

The RAS (figure 12) is a matrix or network of cells extending from the anterior part of the spinal cord into the thalamus. It receives collateral fibers from afferent tracts as they proceed toward the thalamus, and all the receptors contribute inputs to it, directly or indirectly: hence it is a center, or group of centers, on which information from every sensory modality converges. There are also cortico-reticular tracts, both from the isocortex and the limbic system. As for outgoing connections, there is a substantial diffuse projection system of fibers from the reticular substance to the whole of the cortex; this is in contrast to the more familiar specific projection system carrying the sensory inputs, via the thalamus, to the special sensory regions.

Although the RAS is often spoken of as a single entity, in fact it has (i) a posterior part in the medulla and cervical cord, (ii) a central region and (iii) a thalamic reticular system. Injury to the central part, which lies largely in the midbrain, causes coma. This region of the RAS is believed to maintain a tonic, that is, continuous stimulation of the cortex, while the thalamic RAS is supposed to produce the kind of momentary, phasic arousal due to sudden disturbance. But animals comatose through injury can be kept alive if tube-fed; gradually, during several weeks, they become responsive, until they can stay awake without special simulation. Hence tonic arousal *can* occur without the intact central RAS [638].

Evidence on the role of the RAS does not depend only on the results of injury. Consider a sleeping animal of which the EEG is being observed and in which an electrode has been implanted so that the RAS can be stimulated. When the current is switched on, the EEG alters to that of an awakened animal, and the animal may indeed wake up and become responsive to its surroundings. The recording of impulses in various parts of the brain shows that a sleeping or anesthetized animal still receives the input in the specific afferent tracts from the exteroceptors, but that the diffuse projection system is silent: evidently responsiveness depends on the additional cortical facilitation provoked by impulses from the reticular system.

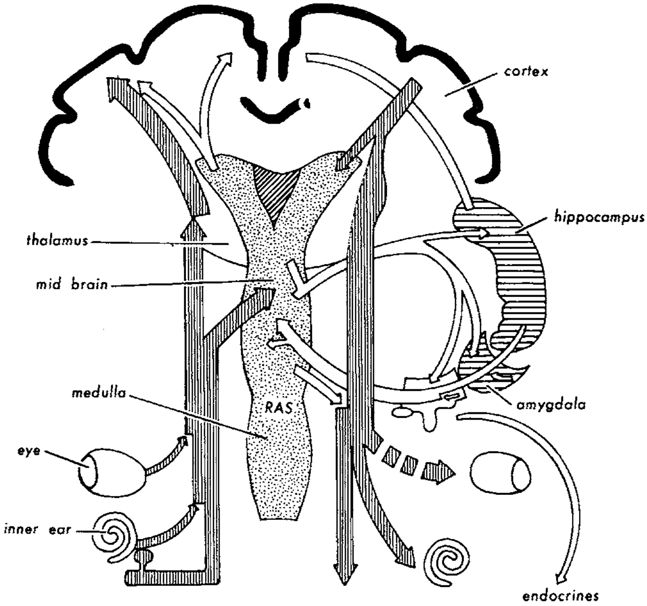


Figure 12. Some of the connections of the limbic and reticular systems. RAS = reticular formation.

As might be expected, the RAS, though described as activating, is not only stimulatory in function: its influence can be inhibitory; this applies especially to the anterior (thalamic) and posterior (medullary) regions. Stimulation of the thalamic portion may bring about the arrest reaction, that is, immobility such as is often seen in an animal suddenly disturbed.

2.6 THE HYPOTHALAMUS

The hypothalamus (figure 11) may be regarded as the front part of the autonomic, or visceral motor, nervous system and also of the less well described visceral sensory system. It has complex connections, both afferent and efferent, with the cerebral hemispheres and the thalamus. It is the most vascular part of the brain, and it probably responds directly to changes in the blood composition. Inject exceedingly small amounts of sodium chloride solution into the hypothalamus, and the animal will begin drinking when it had previously refused water. Electrical stimulation of parts of the anterior hypothalamus may influence the functioning of the gut, for instance, peristalsis; stimulation of posterior regions can alter blood pressure and other aspects of the internal state. The anterior is then especially related to parasympathetic function, the posterior to sympathetic.

The hypothalamus is not regarded as a "reflex center": the visceral sensory tracts end lower in the brain stem, and the visceral motor tracts which pass to motor neurons in the spinal cord also take origin further back. The hypothalamus evidently activates or inhibits reflexes; but it does more. Local stimulation may set going complex patterns of behavior: one example is attack, which is associated with sympathetic stimulation; another is the whole sequence of activities involved in feeding (parasympathetic).

The hypothalamus is also involved in the inactivity of sleep: according to Nauta, the posterior hypothalamus contains a waking center, and the anterior, a sleep center [496]. In Nauta's experiments the hypothalamus of rats was completely cut across on both sides: the result was loss of the normal regulation of sleep. Another maintenance function, thermoregulation, also depends on the hypothalamus: stimulation of the anterior may activate changes which lead to loss of heat, such as peripheral vasodilation, sweating and panting, while the posterior directly regulates the increase of heat production and other processes normally evoked by exposure to cold. The hypothalamus evidently responds directly to the temperature of the blood. If a minute metal probe is used to alter the temperature of the hypothalamus, the animal behaves as if the temperature of the whole body had been raised or lowered [425, 495].

2.7 CONCLUSIONS

The difficulties we meet in the study of the nervous system do not oblige us to reject study of the brain as a source of knowledge about behavior. To do so would be analogous to refusing to study the kidney when investigating the composition of the urine.

The brain, however, presents more difficulties than the kidney. Elementary accounts of the nervous system tend to conceal this fact. For one thing, they often speak of the "functions" of parts of the brain in a misleading way. Three of the preceding sections are headed with the names of structures, but this anatomical arrangement does not correspond to the facts of function: the study of any one of these systems soon becomes meaningless without reference to the others. During every few milliseconds, in the waking brain, information passes to and fro in a network of communication of which only the larger details are yet certainly known. In every specious present, the picture of the outer world which reaches the CNS from the senses is subject to a system of editing or selection and is also imposing changes, more or less lasting, which affect subsequent behavior. In such a flux we cannot, with our present knowledge, properly speak of local function, but only of the specific effects of injury or stimulation. The fact that, say, feeding behavior is altered by damage to a single structure by no means signifies that control of that activity is localized there: it tells us only that the structure is necessary for the normal performance of the behavior. A small injury can influence an activity which certainly depends also on the functioning of other parts; by contrast, some substantial injuries leave behavior largely unaltered; and, when behavior is disturbed by lesions, there may be subsequent recovery due, perhaps, to some compensatory process elsewhere.

These facts make accounts of neural function in terms of reflex arcs absurd. More positively, they enable us to define some of the problems with precision. Instead of thinking of the animal as a black box with a totally obscured interior, we are beginning to see how the complexities of overt behavior can be illuminated by nerve physiology.

3 Movement in the Living Space

And found no end, in wand'ring mazes lost.

Milton

3.1 Range and Territory

An animal species has a geographical range within which it occupies one or more habitats: habitats occupied by rats include agricultural land and built-up areas. A habitat may be divided into biotopes, such as hedgerows and warehouses. Within these are colonies of rats; and each rat has a region in which it moves—its *home range* [347]. The home range of wild rats is probably quite small. It was studied by D. E. Davis and his colleagues in Baltimore and on a farm: in the city they trapped rats, marked, released and recaptured them; for 80 percent of the rats the distance between first and second captures was less than twenty meters. They also put a dye in rat bait: the distribution of colored dung around the bait stations indicated a range of about thirty meters in diameter [186]. If an animal, a pair or a group occupies a region from which other members of its species are excluded, that region is a *territory*. Rats are territorial animals, but for males the relationship of territory with home range is not known. For female *Rattus norvegicus* the territory, when there is one, is probably the nest.

The main subjects of this chapter are the movements of rats about their living area and the experimental analysis of the causes of movement.

3.2 Analysis of Activity

3.2.1 The Causes of Activity

3.2.1.1. *Methods.* Rats move about when they are getting food or water or nest material; when they are finding a mate or a site for nesting; and when they are fleeing from a predator. But their movements are often by no means obviously related to such activities. To what extent are rats' movements determined by immediate need?

Laboratory rats have long been described as highly exploratory and inquisitive. One of the earliest studies, that of Small, published in 1899, describes this behavior at length and refers to the restlessness of infant rats as "premonitions of curiosity" [618]. Wild rats, too, are actively exploratory, though this is often obscured by a form of "wariness" which laboratory rats hardly display (§ 3.3). Generalized movement about a substantial area can, however, easily be observed in wild rats given access to a strange place: this can be arranged by removing a barrier which has hitherto prevented entry by rats living on adjacent ground [60], or by putting rats in a large and unfamiliar cage [47].

Sometimes it is possible to account for the movements of an animal in common sense terms. In natural conditions, and in captivity also, activity may seem obviously to spring from some internal deficit: after an interval without food or water, an animal which has been sleeping or resting goes to a place where it can eat or drink. But not all the ranging movements of rats can be explained in this way. Consider, for instance, rats which have been deprived of food for twenty-four hours. While they are resting in the back of their cages, food is put at the front where it has been given before. Soon the rats become active and begin to eat. When they have eaten a good deal and have drunk some water, they carry out a general exploration of the cage [36]. Evidently, in this situation, exploration comes *after* a deficit has been made up.

To study the many factors which influence "activity" we need to record movement quantitatively. Bindra [95], Bolles [100] and Gross [273] have reviewed the attempts to do this. We shall see that different devices measure different phenomena; and, more important, we shall find ourselves obliged, if we wish to achieve rigor, to discard the unqualified term "activity" and to analyze the movements of animals into components precisely defined in terms of the procedures used and the observations made.

The earliest quantitative studies were of rats in small cages; each communicated with a wheel or treadmill in which the rat could run; revolutions were recorded by a cyclometer. The method allows continuous recording over days or weeks, during which the animal need not be disturbed by the experimenter. Activity so measured varies with internal state, for instance, with the stages of the estrous cycle (figure 13). The animal is, however, necessarily isolated from others, unless special arrangements are made to give it a companion that cannot enter the wheel; and prolonged isolation has a distorting effect on behavior (§ 5.4). A wheel also has effects unlike those of other devices for measuring activity: its presence, or its movement when running has begun, provokes further running: activity, in the sense of distance covered, is much greater when a wheel is present than in a simple cage, especially when the animals studied are in a state of deprivation, as from a fast [705]. The details of the design of the apparatus may also influence the response to it: Kavanau offered deer mice, *Peromyscus*, a variety of wheels. Those of more complex structure induced the most running: for instance, the mice preferred to run in a wheel which offered hurdles to jump over, rather than in a plain one [354].

Collier & Hirsch have studied wheel-running from a different point of view. They trained rats to press a lever to release a wheel; the opportunity to run in the wheel then acted as a reward, just as food does to a fasted rat. These authors hypothesize that running is a regulatory activity: specifically, that it helps to maintain body fat stores in a steady state [163].

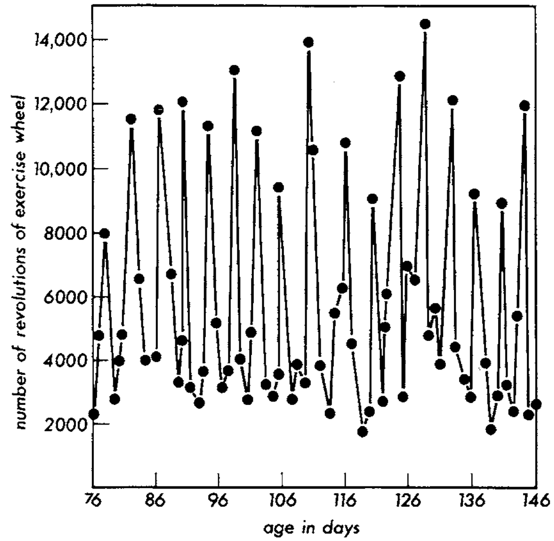


Figure 13. A behavioral cycle. The four-day estrous cycle of the laboratory rat is accompanied by changes in the amount of running in an exercise wheel. Peaks of activity accompany estrus. (After Richter [545].)

The running wheel may be compared with another device for recording activity continuously. Cages mounted on tambours or, more recently, on micro-switches or pressure transducers have not the stimulating properties of running wheels. A rat given a wheel may not settle to a steady running rate for some weeks, but it habituates to a mounted cage in a few days at most [273]. A still more advanced technique employs a tuned oscillator circuit which records movement in its electromagnetic field [356, 661]. Just what is recorded by these methods may be difficult to define precisely: it may be described as gross locomotor activity in a circumscribed region (a cage).

The two classical methods, the wheel and the mounted cage, give very different experimental results. J. McV. Hunt & Schlosberg castrated rats and recorded a 95 percent reduction in wheel-activity; but the reduction in cage-activity, when the cage was on tambours, was only 9 percent [341]. Correspondingly, brain injuries which depress wheel-activity may not affect cage-activity [203, 420]. Kršiak and others have studied the effects of drugs on response to a novel environment, and have recorded still further complications. Correlations between behavior directly observed and that recorded automatically broke down when the activity of rats was altered by amphetamine [383].

A cage, with or without a wheel, is a very restricted environment. For a burrowing animal, such as a rat, a system of branching passages, or maze, seems a more natural situation. But in their usual form mazes are designed to allow an animal only a brief stay. It is, however, possible to design an artificial, structured environment which, with electronic equipment, allows a record of an animal's movements over a long period. Kavanau has done this on an elaborate scale for his observations on deer mice [355–56]. A simpler (and less expensive) residential maze is illustrated in figure 14: a central nest box leads to four arms, of which each may contain an incentive such as food, or may be left empty. Infra-red beams cross the arms and allow the recording, from moment to moment, of both visits to the arms and also duration of stay in them. The recording devices have no effect on the animal. The number of arms and their structure can, of course, be varied. By this arrangement, changes in behavior with internal state, such as those of pregnancy and lactation, have been described (figure 15). If another animal in the nest box were prevented, by a tether or collar, from entering the arms, movements of one individual could be recorded in a social situation; it would then be necessary to supply both food and water in the nest box.

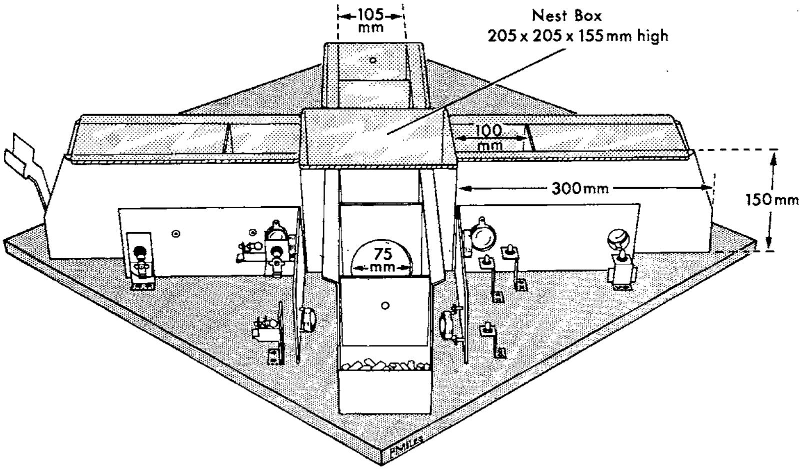


Figure 14. Residential maze in which visits to the arms and duration of stay in them are automatically recorded. This maze is designed for rats. Smaller ones are used for mice [55]. (From Barnett *et al.* [58].)

To study animals in less artificial conditions, still more elaborate equipment is needed. It is possible to fasten miniature broadcasting devices to an animal, and to pick up the signals with a receiver which plots the animal's movements (telemetry). In this way a small mammal could be allowed to construct its own maze (or burrow) while under observation.

3.2.1.2 *Deprivation.* Deprivation of food or water, departure from a particular range of environmental temperatures, and other potentially injurious circumstances would be expected to lead to increased movement: in natural conditions, movement improves the chances of an animal's restoring its state to the optimum. The preceding statements concern the survival value of behavior, that is, its function. They say nothing, however, of how the movement is brought about, or just what form the movement takes.

Before these questions of mechanism can be examined, we need to be quite certain that "activity" does increase when an animal is in a state of deficit and, if so, "activity" in what sense. This apparently simple question has proved to be not simple at all. The first experimentalists had few doubts. Often, they used a running wheel: for instance, Wald and Jackson increased wheel-running by rats by depriving them of water, or food and water, or thiamin (vitamin B_1); but this type of experiment measures response to a wheel, not movement about an environment [697]. Fehrer, by contrast, observed rats in cages so arranged that, at a chosen time, the experimenter could give a rat in its nest box the opportunity to enter another compartment. Rats were more likely to leave the familiar part of the cage if they had been deprived of food for some time [234]. Similarly, P. S. Siegel & Steinberg recorded the movements of rats by means of light beams across their cages: activity so measured increased at a regular but declining rate during a fast of 48 h [611].

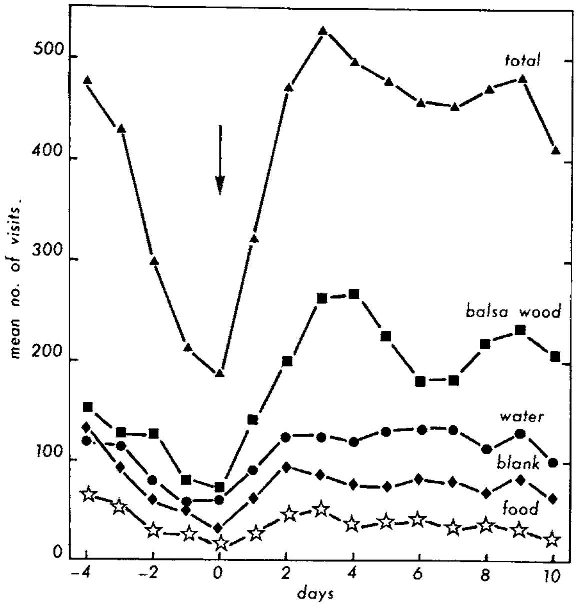


Figure 15. Record of activity (movements) of twenty mice during late pregnancy and lactation, in residential maze (see figure 14). The four arms offered (i) food, (ii) water, (iii) balsa wood, which was gnawed or used in nest-building, and (iv) nothing. (After Barnett & McEwan [55].)

Some observations, then, accord with common sense. But in other conditions, in a simple, structured environment, rats move about *less* when they have been for hours without food or water than when they have had continuous access to both (figure 16) [161].

Many further studies, reviewed by Bolles [100], have failed to reveal any firm rule. One reason for conflicting findings is that "activity" has meant different things in different researches. Another is that, even in a single study, it may be difficult to decide exactly what is being measured. This is illustrated by the work of a physiologist, S. D. Morrison, who recorded the movement of rats by a sensitive micromanometer: locomotion in a small chamber caused small alterations of pressure which were detected by a capsule; this was connected to apparatus adjusted so that the normal movements of breathing were "barely detectable"; the apparatus also allowed estimation of total energy expenditure. In these conditions "total spontaneous activity" (which included feeding behavior) used a constant proportion of total energy expenditure of about 25 percent. Fasting did not induce greater activity in this sense, but only an increase in non-feeding movements [482].

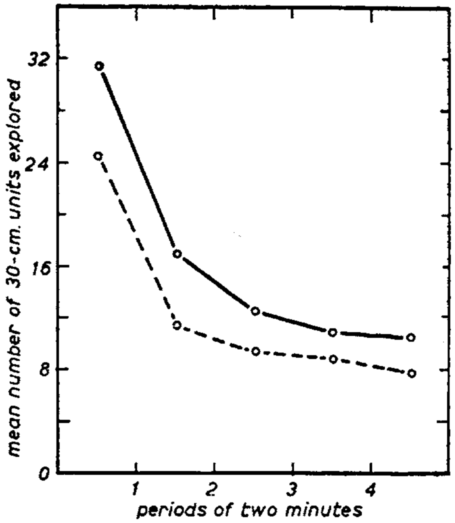


Figure 16. Effects of hunger and thirst on exploratory behavior. Sated rats (continuous line) explored more than rats which had been deprived of food or water for some hours (broken line). In different conditions contrasted results may be obtained, as in figure 17. (After Montgomery [473].)

Another source of inconsistent results can be the history of the animals observed. Bolles & De Lorge put rats in a complex maze; some had previously had experience of being deprived of food; others—the controls—had not. The previously fasted rats, though not deprived at the time of the experiment, moved about more than the controls; if, however, they were observed in the maze while fasting ("hungry"), they were not more active than the controls [101].

The quality of early nutrition can also influence movement in an environment of the kind shown in figure 14, even when the animals are studied long after they have been restored to a complete diet. Rats which have had a low-protein, high-carbohydrate diet for a few weeks after weaning are more active in such a plus-maze, in the sense of making more entries to the maze arms, than rats which have been undernourished or have received a complete diet all their lives. By contrast, formerly undernourished rats spend more time in the arms than either of the other groups. Hence, in these experiments, time spent out of the nest did not necessarily correlate with "activity" [58].

3.2.1.3 *External stimulation.* It is common sense that changes in internal state will alter some kinds of activity. Only the uncommon sense of the inquiring experimenter reveals the difficulty of making that statement precise. It is equally obvious that external stimulation can make an animal active. This section deals with the question whether external stimulation contributes to the increased activity which sometimes occurs during deprivation.

Consider the sleeping or resting animal. At a slight sound the animal wakes and moves. The movement may be toward the source of the sound, or away from it, or neither. Whatever its direction, we may ask whether the state of the animal alters its responsiveness to disturbance. Campbell & Sheffield studied rats in stabilimeter cages kept in a room in which sights and sounds hardly varied. Since complete quiet can be achieved only with great difficulty in a room containing animals, a steady "white noise" was maintained. In this constant environment, fasting had little effect on cage-activity. But on each day, for ten minutes, the noise was switched off and bright lights were switched on. This always evoked greater cage-activity; and the effect of environmental change was much enhanced by deprivation [132]. In a later study, fasting led to a 10 percent increase in cage-activity in a uniform environment, but a 400 percent increase in an ordinary laboratory [663]. Wheel-activity is similarly influenced by flashing lights and noises, especially when the animals have been fasted [283]. Indeed, the effect of a deficit on activity is much greater when measured by wheel-running than by cage movements [273]. This is perhaps because the wheel itself provides external and kinesthetic stimulation.

In yet another investigation, in a more complex environment, the movements of rats were observed in a cage with two compartments connected by three doors. To cross from one compartment to another, a rat had to find the one door which was unlocked. The number of crossings was increased by both a bright light and food deprivation. But, even in the absence of either, many crossings were made (figure 17). In these experiments, then, the effects of light and of fasting were superimposed on a tendency to explore regardless of the particular circumstances.

This observation suggests a new possibility, namely, that rats tend to be active regardless of specific stimulation. If so, as with behavior such as eating, deprivation might be expected to increase activity. Montgomery confined rats in small cages and found no effect on the intensity of subsequent movements in a simple maze [474]; but Hill later reported that confinement was followed by increased motor output in mounted cages [322]. The difficulties of interpreting these experiments have been discussed by Lore [419]. He finds no evidence of a consistent relationship between restriction and subsequent movement. He emphasizes that restriction can have adverse physiological effects (he calls it a stressor). If prolonged, it can result in a permanent change in an animal's response to novelty.

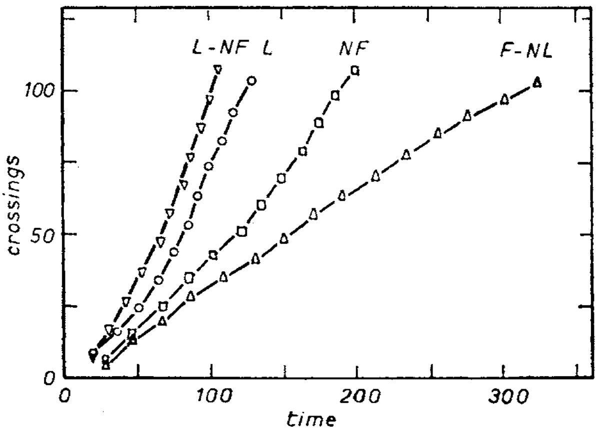


Figure 17. Effects of hunger and strong light on activity. Light (L) and hunger (NF) both increased the rate at which the rats in one box crossed into another, connected box; but even the rats which had been fed and were not exposed to light (F-NL) crossed often. The graphs show mean number of crossings against time in minutes. (After Jerome *et al.* [346].)

There is, then, at present no adequate ground for speaking of a general activity drive, even if that term were precisely defined. The activity of rats, measured in a cage, a wheel or some more complex environment, may be increased in at least four ways. First, changing stimuli, acting on the exteroceptors, increase activity. Second, some kinds of constant external stimulation, such as a bright light, may do so, since bright light is generally avoided. Third, deprivation of food (a) lowers the threshold of response to external change, (b) may itself increase movement in a constant environment. Fourth, a raised concentration of certain hormones, especially those of the gonads, in the blood stream may be accompanied by a rise in activity.

3.2.1.4 *The circadian rhythm.* One of the meanings of activity is absence from the nest or lair; the period of activity so defined may coincide with the period spent moving about, eating or drinking. In either case, the activity of rats, as of other nocturnal mammals, displays a circadian rhythm, that is, a regular cycle of change in every twenty-four hours (reviewed by Harker [288]). There is usually little activity during the light hours; but around sunset (or its laboratory equivalent) the animals emerge, and spend much of the first hour or two of darkness outside. After this peak, there may still be a quite high, though fluctuating, level of activity during the night, with a probable second peak shortly before dawn. Most feeding is during the night, but this can readily be altered if food is more easily gained at other times (§ 4.4.3.1).

The circadian rhythm of overt behavior is accompanied by a syndrome of internal changes. Metabolic rate, for example, measured by resting oxygen consumption, is about 25 percent higher during the night than during the day [320–1].

The circadian rhythm may be important in the design of behavioral experiments. This may be exemplified from experiments in which rats are strapped up for some hours so that they cannot move. Animals so immobilized sometimes develop injuries of the gastric mucosa, but there is much variation in the incidence of the lesions. As Ader has shown, one source of variation can be the time of day, or—more precisely—the phase of the circadian cycle, at which the treatment is imposed: the ill effects are greatest if the animals are immobilized at the time when they would normally be most active [4, 7]. Hence experimental treatments and behavioral observations should be made at a fixed time.

Other features of circadian rhythms are discussed in § 4.4.3.1.

3.2.2 Spontaneous Alternation

We now return to the features of the environment which influence an animal's choice of pathway. An animal such as a rat moves about its home range even when there is no evident internal state or external stimulation to provoke movement. What determines this activity? And what, at any given moment, determines the choice of direction? Such questions are usually discussed under the heading of "exploratory behavior"; and some of the answers have arisen from experiments on spontaneous alternation. This phenomenon is readily displayed in mazes in which the animal is *not* rewarded on reaching a goal. The maze need have only one point at which a choice of routes must be made (figure 18). It is then easy to express the animal's responses quantitatively. In such a **T**- or **Y**-maze, rats given two runs in rapid succession tend on the second occasion to make the choice not made on the first run: if they turn left the first time, they will probably turn right on the second run. The same sort of behavior can be observed in more complex mazes. Further, the more complex a maze, the greater the amount of movement in it (figure 19).

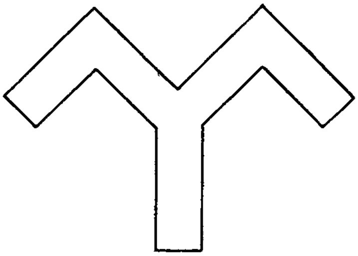


Figure 18. Plan of **Y**-maze. Each arm is about 300 mm long.

Spontaneous alternation may be regarded as a special case of exploratory behavior, since it tends to increase an animal's range of movements. Hence an analysis of alternation is likely to throw light on exploration in general. According to an early hypothesis, rats tend to vary the *response* made in a given situation: on this view, the performance of a movement induces a state of "reactive inhibition" which for a short period prevents the repetition of that movement. The inhibitory effect, whatever its nature, dissipates gradually. In an investigation by Heathers, one group of rats had an interval between choices of 15 seconds, while another group had to wait 120 seconds: in the first group alternation between the two possible paths occurred in 83.5 percent of trials, while in the second the percentage was only 65.6 [303].

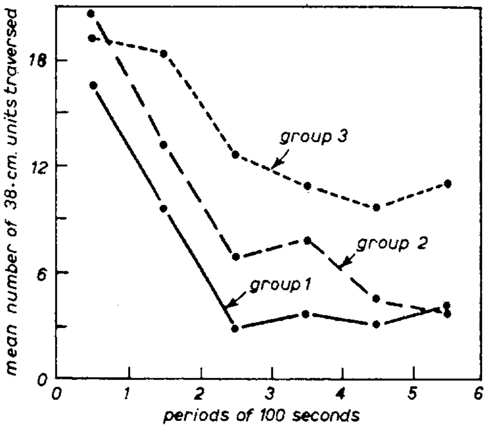


Figure 19. Effect of complexity on exploratory behavior. Rats were put in an I-maze (group 1), a L-maze (group 2) or a T-maze (group 3): the more complex the maze, the greater the amount of movement. (After Montgomery [471].)

Such behavior need not, however, be due to inhibition of the response: the animal might be varying the *stimuli* received from one choice to the next. On this view the animal behaves as if it were bored with one part of the maze and therefore turns to another: it avoids not a response just performed, but stimuli recently experienced.

Is the behavior in fact response alternation or stimulus alternation? This question has been investigated, by Walker and others, who used cross-shaped mazes which can be rotated so that any of the four arms can point toward any feature of the laboratory; the arms of the maze are painted black or white, and any arm can be blocked so that the cross can be converted into a **T** (figure 20). With this equipment the effects of three factors can be distinguished: (i) the response, that is, turning left or right; (ii) the visual stimulus provided by the differently painted arms of the maze; (iii) the visual stimulus provided by the background outside the maze. On any given occasion the maze can be arranged so that a rat has a choice between alternating (i) its response, or (ii) the input from some aspect of its surroundings. In these conditions, the rat varied the visual stimulus it received on successive choices, but showed no tendency to vary the response, that is, to alternate between turning right and turning left. The effects of the color of the maze and of the laboratory background were about equal [700].

An important feature of spontaneous alternation is then avoidance of external stimulation recently received in favor of stimulation that is either novel, or, at least, less familiar. This notion is further supported by experiments by Sutherland. He used a modified **T**-maze in which the alternative paths could lead round either to the same goal box or to different goal boxes; in the second case the two boxes were of different shapes. Alternation was more frequent when the goal boxes were different [658].

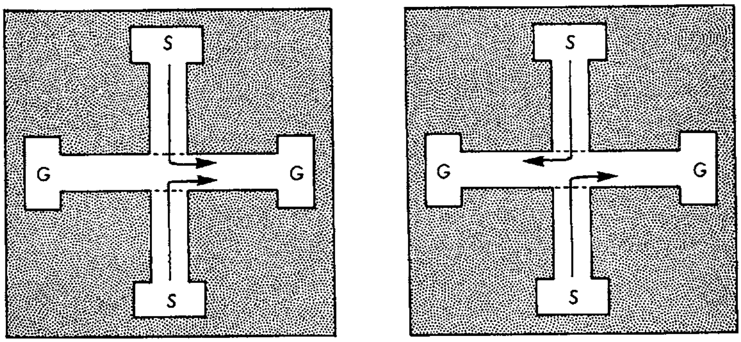


Figure 20. Test for stimulus alternation versus response alternation. On left, arrows show direction of rat's movement, on successive trials, when the *response* is alternated; on right, place or stimulus alternation is shown. S = start; G = goal box. (After Montgomery [472].)

When we try to decide just what stimuli are influencing an animal hesitating at the choice point of a maze, it is easy to overlook the possibility that, during a previous run, the animal itself has significantly altered the maze. Douglas has brought evidence that spontaneous alternation includes a tendency to avoid the odor-trail left on the previous run [207]. In some types of experiment it is clearly desirable to control for this factor.

Nevertheless, despite the importance of external stimulation, in some conditions alternation may be determined partly by the actual movements made. A maze was used in which the entries to the goal arms were complicated: each involved twists of the rat's body and changes of direction, and the contortions required were quite different in the two arms. The tendency to display response alternation was then nearly as marked as that to display stimulus alternation. Perhaps a relevant factor is the readiness with which alternatives can be discriminated: merely turning left or right are not very different, but one set of contortions is easily distinguished from another [699].

An important question is whether response alternation and stimulus alternation both reflect a single fundamental process. Dember put rats in a **T**-maze in which one goal arm was painted white and one black, but the rats were prevented by glass barriers from entering either arm on the first run. On a second exposure, both arms were painted the same color (black *or* white), and either could be entered. Most of the rats explored the *changed* arm [193]. This observation emphasizes the importance of *novelty*. Evidently alternation is an expression of a tendency to behave so that the input to the central nervous system is varied. This input may be through exteroceptors, as in the usual situation, in which the visual stimuli differ; or it may be through proprioceptors, as in the case of response alternation.

The novelty principle perhaps applies to all kinds of stimulation. Wild rats given a choice of three or four foods nearly always sample them all during a feeding period, even if one is more readily eaten than the rest. The sampling tends to occur after a period of feeding on the preferred food [36]. Welker & King scattered familiar and novel food pellets and other objects about the cages of laboratory rats. The rats ate more of the unfamiliar food, and paid more attention to unfamiliar inedible objects than to those already experienced. These observations were repeated daily, until by the fourth day the amounts of the two kinds of food eaten were equal [711]. Further relevant evidence comes from neurophysiology. Horn, in a discussion of selective perception, remarks that novel stimuli have a high probability of producing central nervous arousal [332].

3.2.3 Attention to Change

Studies of movement in other experimental situations strengthen the emphasis on variety of stimulation. A laboratory rat faced with a small enclosure containing objects of differing familiarity spends more time exploring the new things. A decline in the "interest" or "attention" aroused is observed even when an object is presented only for the second time [87]. If this is boredom, these observations suggest that rats are very easily bored.

It is, however, more profitable to analyze further the precise features of the situation to which the rat is responding. When a rat enters, or is put into, an enclosure containing various objects, it approaches, sniffs and perhaps licks or gnaws them; it also moves around the whole enclosure. What exactly makes it do so? We have seen that novelty in the stimuli presented is one factor. The importance of novelty alone has been most clearly shown by presenting laboratory rats with a variety of visual patterns. Montgomery exposed cards with different black and white patterns on the walls of a simple maze. Given this stimulation, rats explore (that is, sniff and move around) more than control rats exposed only to a constant stimulus. But another aspect of some of the stimuli that evoke exploration might be their complexity; and a third factor might be the spaciousness of the area available for exploration. Berlyne & Slater have tried to distinguish these three. First, rats in a **Y**-maze were found to sniff at an unfamiliar patterned card more than a familiar one; this confirmed what was already known. Next, one goal arm of the **Y**-maze was given a more spacious goal box at the end, and this was entered more frequently than a simple blind alley. Third, complex stimuli were compared to simple ones by means of cards, some of which were plain, others patterned; altering a pattern was more effective than merely changing from black to white or white to black [90].

Although novelty, complexity and spaciousness, separated in this way, seem very distinct, they probably all act in the same way [96]. A rat in a maze may be regarded as scanning the total situation, not only with its eyes but also with its other exteroceptors; the greater the complexity of the stimuli it scans, and the more spacious the area accessible to its senses, the greater the variety of input through its sense organs.

These notions, too, have been tested in mazes with a single choice point. Animals can be trained to turn always (or nearly always) left in such a maze, if they are rewarded with a fragment of food on that side and given no incentive on the other side. What happens if, instead of some obvious reward, the animal is given an opportunity to explore? In such an experiment, turning in one direction may lead to a blind alley, but turning in the other leads to a larger, and (as we may think) more interesting, area. In this situation the rats do not alternate, as they do when there is no reward in either of the arms, but develop the habit of following the path which leads to the larger space [475, 492]. Spaciousness itself is not a necessary feature of the reward: merely presenting novel visual stimuli is also effective [149, 370].

Nevertheless, it might be thought that spaciousness is in a special category, since the tendency to choose the larger of alternative areas might reflect an attempt to *escape*. This suggestion is worth discussing, since it illustrates a point of method. For a man, to escape is to move permanently from some confinement to a preferred place. But when a rat explores an area, familiar or not, near its nest, it typically returns in the end to its starting point. This is well seen in wild rats that have "escaped" from a cage, either by the design of the experimenter or against his wishes: they usually return to the accustomed nesting site, or other cover nearby, to sleep. If an animal permanently leaves its home ground, and one wishes to explain this, it is not adequate to say that the animal "wished to escape": it is necessary to say *from what* it was "escaping"; the provocation may be a state of deprivation, for instance of a mate, or some positively disadvantageous feature of its home, such as continual disturbance by man or by a hostile companion. The suggestion of escape, unqualified, is an anthropomorphism. It is based on the fact that most human beings tend to avoid being confined in a small space. By contrast, as Hediger [313] has pointed out, many animals, if provided with all their obvious needs, show no impulse to leave cages or enclosures permanently.

3.2.4 Stimulation as Reward

The facts outlined above have led some psychologists to use expressions like "stimulus hunger" and "curiosity drive" to refer to the internal springs of exploration.

Positive reinforcement may be of two kinds, primary or secondary. Food is an example of the first; opportunity to visit a place where food has previously been available could be a secondary reinforcement. Montgomery & Zimbardo have raised the question whether exploration represents secondary reinforcement, since in early life such behavior must have preceded the finding of food; perhaps exploratory behavior is a habit developed at the time of weaning [476]. If so, exploration should decline in intensity when it is not rewarded by food or something equivalent, that is, it should undergo extinction (§ 8.5); but it does not do so. In a constant environment, apparently unrewarded movements about a living space are repeated day after day. Fluctuations in their intensity may reflect changes in the animal's internal state (figures 13, 15, 16); but the animal shows no sign of developing a lasting state of boredom. Similarly, experimenters have usually found no evidence of a decline in spontaneous alternation when the runs were repeated. Alternation certainly differs in its persistence from a habit developed by training with a typical reward, such as food. But in experiments by Still, in which rats were run for longer than usual, alternation did diminish. Further study is needed: perhaps secondary reinforcement sometimes plays a part in exploration generally and in alternation in particular [650–52].

Novel visual stimuli, and access to a large space, are not the only situations which possess an unexpected rewarding property. This has been shown in experiments with Skinner boxes (§ 7.2.1.3). The rat has access to a lever which, when pressed, releases a reward such as a pellet of food (plate 24): it soon learns to press the lever and to enjoy the fruits of doing so. Kish & Antonitis observed the performance of rats when the lever produced nothing more interesting (to man) than a clicking noise. This proved to have a rewarding effect: it induced rats to press the lever more often than when the result was silence [371]. The incentive to press a lever was then only minor stimulation of an external sense. Perhaps rats tend to behave so that, within a given period such as twenty-four hours, they achieve a certain level of central nervous excitation via their exteroceptors. Such a notion is neurophysiologically not very precise, but it has led to the hypothesis that, if one sensory modality is put out of action, greater activity should result. Accordingly, Glickman blinded rats of a strain with good eyesight: when they had recovered from the operation, the animals explored more than sighted controls [261], and so seemed to be working for stimulation.

There have also been many studies on the effects of switching a light on or off. Rats (and deer mice [355]) work for either. If this represents working for stimulation in general, and not for the opportunity to see around, then animals should also work to switch a light *off*. Glow found both light-off and light-on to be reinforcing: that is, his rats worked for both. But they worked more for light-off, especially when they had been in the experimental situation for many minutes [262]. Detailed analysis reveals many further complexities. Donahoe gave rats the opportunity to switch on a light in apparatus in which the light alternated between two positions; more response was provoked than when the light was always in the same position [205]. D. I. Williams & Lowe similarly found a greater response to a flickering light than to a steady one [716].

The movements of an animal are often directed toward the achievement of objects or conditions needed with some urgency for survival, such as food or shelter. The work on exploration as reinforcement indicates that rats are impelled to explore, just as they are impelled to find and eat food. Sometimes exploration even has priority over other activities that seem more important for survival.

Wild rats ordinarily take cover when disturbed but, if they are placed in a completely unfamiliar enclosure, they usually explore it before settling in a concealed place. The explanation is not that they have had no previous experience of where cover is to be found: in large cages fitted with nest boxes, the boxes may be visited during the exploration; but the rats are evidently so stimulated by the new surroundings that they emerge again, despite the presence of the experimenter, and resume their wanderings. Later, when the conditions are familiar, exploratory movements are repeated at intervals, but only when there is no disturbance [47]. Similarly, a male rat, placed in a cage already occupied by other males, may persist in leaving cover and exploring, even though it provokes repeated attack.

Comparable observations have been made in more formal experiments on laboratory rats. Figure 21 shows a checkerboard maze, in each of whose squares there is a cup which may hold food or water. Rats were deprived of water and then placed in the maze with water or food in the cups. The water-deprived rats explored for many minutes before drinking, and food-deprived rats for still longer before eating. The same principle is illustrated by a maze with a conventional starting point and a goal, but so designed that the arrangement of the passageways can be altered between runs. In the maze shown in figure 22, hungry rats tended to choose the *longer* of alternative routes to food, provided that this route was *changed* between successive trials.

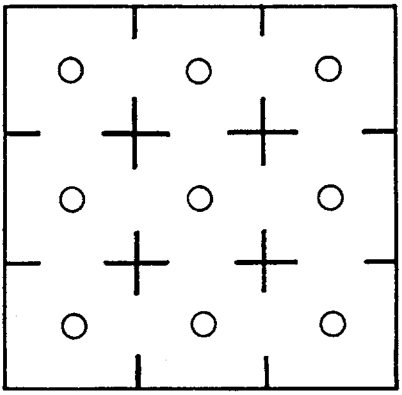


Figure 21. Checkerboard maze, with a cup in each unit, used for studying the effect of the presence of food or water on exploratory behavior. (From Zimbardo & Montgomery [738].)

The movements of rats, then, include as an important component responses to variation in their surroundings; the variation may be in time or in space; it may consist of an opportunity to move around in new areas or only to perceive new stimuli. There is a strong neophilic tendency, or active seeking of variety. Neophilia is by no means confined to rats or even to rodents. Analogous behavior by rhesus monkeys (*Macaca mulatta*) has been studied in detail: these creatures are strongly visual, and will spend much time and appreciable energy in merely watching a scene with plenty of movement [120]. Chimpanzees (*Pan troglodytes*), as would be expected, are also neophilic [710]. Exploratory behavior is important for many, probably all, other mammals. Apart from those already mentioned, however, only a few, such as the domestic dog, have been formally studied [673]. There is a dearth of information on other vertebrates, though birds are certainly exploratory; for information on them, and on invertebrates, Thorpe [676] should be consulted. Exploratory behavior is evidently a widespread phenomenon in the animal kingdom.

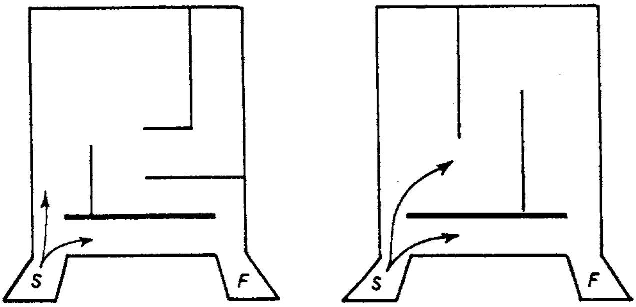


Figure 22. Maze which provides alternative routes to the goal. If the longer one is varied (compare the two diagrams), a rat tends to prefer it to the shorter. (After Hebb & Mahut [311].)

3.3 NEOPHOBIA

Wild rats, though highly exploratory, do not always respond to novelty by approach; and even a laboratory rat may freeze, or pause in its movements and groom itself, when faced with something strange [95]. In colloquial terms, we might attribute these responses to fear. Berlyne [87–9] has written fully on the aversive effects of unfamiliarity. The response to novel stimulation, he suggests, depends on two factors: (i) the initial state of arousal of the animal; (ii) the arousal value of the stimulus. These determine whether the reward system or the aversion system of the brain is the more active. His evidence is behavioral, and largely from experiments on laboratory rats. In some experiments he used a Skinner box (plate 24). Pressing the lever switched on either a light or, briefly, a buzzer. As we know, rats will work even for such meager rewards. The experiments were done in two conditions: in one, the animals were in quiet surroundings; in the other, there was continuous noise. In the quiet, the light or the buzzer were more effective as rewards if they were completely unfamiliar; but in the noisy environment the animals were more ready to work for light or sound if they had already experienced the light or buzzer. The assumption is that the general noise induced such a state of arousal in the animals, that the additional arousal of a novel stimulus tended to be aversive. Further evidence comes from experiments by Berlyne in which a stimulant, amphetamine, was used to increase "arousal": rats which had received the drug responded at a higher rate when the stimuli were familiar, while control animals, which received only injections of saline, responded most vigorously when the stimuli were novel.

These findings suggest that there is an optimum level of stimulation or arousal for a given activity, such as pressing a lever. A simple model of this hypothesis is shown in figure 23: performance increases up to a certain point, but the high level is not maintained beyond that point. A curve of this shape could be a result of the varying of only one factor, or it could represent the effect of the interaction of two factors. In the second case, the rising curve on the left would represent increasing reward, while the descending part of the curve would show the action of increasing interference by some aversive process. Such models are fascinating, but explain nothing: they are means by which actual findings may be summarized, though there are few authentic examples of such curves; and they can sometimes suggest further experiment. Clearly, we need quantitative information on the underlying processes in the central nervous system.

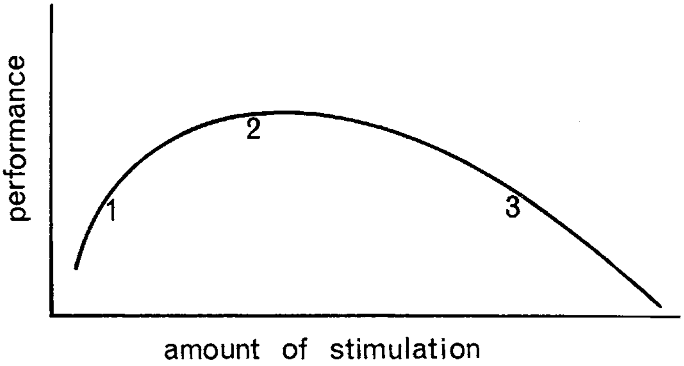


Figure 23. Hypothetical curve: the inverted **U**. If increasing "stimulation" leads to a raised response at first, but then a decline, confusing and apparently contradictory findings may be obtained: for instance, the level of response at points 1 and 3 is the same. A similar effect would occur if the **U** were not inverted.

We now return to the question of "fear": perhaps novel stimuli arouse "curiosity" when they are of no more than moderate intensity, "fear" above that level [87]. But "curiosity" and "fear" are subjective terms: they refer to human feelings. If statements are to be made which can be tested by others, we must again express our hypotheses in terms of observable activities or internal processes. We may therefore talk of approach, sniffing, manipulating and similar acts as counterparts of curiosity, and freezing, defecation or flight instead of fear. We then arrive at a position similar to that reached in discussing Berlyne's hypotheses at the beginning of this section. Moreover, as Halliday [284] has pointed out, situations which induce exploratory movements also evoke such signs of central nervous arousal as defecation and freezing. He suggests, like Berlyne, that the responses to novelty, at least of rats, can be interpreted in terms of two opposing tendencies, which he calls "exploration" and "fear"; once again, the need for more information on the physiology of the behavior is evident.

Laboratory rats are, however, in one way unsuitable animals for experiments on neophobia: decades of breeding in the laboratory have left us with varieties lacking some of the most distinctive behavior of the wild form.

Wild rats are known to farmers, warehousekeepers and householders as wary and elusive animals which can be trapped or poisoned only with difficulty. It is not immediately obvious how this picture, based on millennia of experience, can be reconciled with that of the preceding section, in which rats appear as insatiably inquisitive and, indeed, as compulsively poking their noses into anything new. Certainly, if wild rats behaved in this way on all occasions, there would soon be few left in habitats occupied by man. In fact, they are protected by a type of response which is the opposite of exploratory behavior and which sometimes completely inhibits it.

The behavior was first systematically studied during field researches on methods of poison baiting. Its main features are seen among wild rats settled in an area in which they have established pathways. Use of such a pathway or eating nearby food can be completely prevented, sometimes for days, merely by placing on it some unfamiliar object, such as a box (figure 24). Even a heap of nutritious food may have this effect for a time. "New object reaction" may be evoked also by a familiar object in a new position. Unfamiliar noises have a similar effect, but the extent to which wild rats become habituated to them has not been studied in detail. There is some evidence that unfamiliar odors are aversive [151]. There has, however, been no rigorous analysis of the whole range of stimuli which induce avoidance. The question of what is, for a rat, a "new object" has yet to be fully answered.

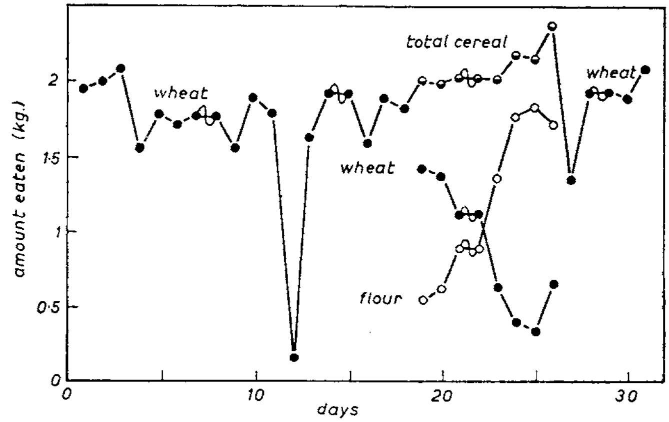


Figure 24. Avoidance behavior of wild rats. The amount of food eaten by a colony of wild rats was recorded daily. From the twelfth day the food was placed on tin trays instead of the floor: this led to a sharp decline in food consumption during the next 24-h period. Making flour available, as well as wheat, had no effect on the total eaten; but removal of the flour after eight days, when the rats had become accustomed to eating it, caused a decline for one day. (After Chitty [151].)

The contrast between wild and laboratory rats has been demonstrated by experiments in small cages, in which the two types (all born and reared in the same laboratory) were subjected to exactly the same conditions. If a wild rat is accustomed to feed from a wire basket at the back of its cage, and food is transferred to an unfamiliar tin in the front, the result may be a complete refusal of food for several days. By contrast, white or hooded rats, faced with the new object, begin to explore it within a few minutes, and their daily intake of food is unaffected. The feeding of a wild rat may even be interrupted if an unfamiliar tin is placed in the front of the cage, without any change in the position of the food; and this interruption is not due to the rat's being distracted by exploring the new object: on the contrary, the tin is for some time completely avoided. In such experiments food consumption is used as a convenient index of neophobia; and in the second kind of experiment the strange object by itself induces a state which inhibits feeding even on the familiar food in its familiar place [38].

Two important features of neophobia must be emphasized. First, it is temporary: although the effect can last for weeks, usually the avoidance is overcome in a few days or even hours. This is an example of habituation (§7.3.2). For habituation to take place, the new situation must, of course, remain unchanged: any other alteration in the environment will drive the rats away again. Such facts have obvious implications if one wishes to deal with an infestation of wild rats, for example by trapping.

Second, neophobia is always observed when there is a *change in an otherwise familiar situation.* Among wild rats, as we have seen, investigation dominates in a totally new environment (new place reaction—an example of neophilia), while avoidance results from a relatively minor change in a familiar constellation. The important factor seems to be contrast between what is expected (that is, what has been experienced before) and what is actually observed. Hebb gives an example of neophobia, similar to that of rats, in his study of the fear and anger of chimpanzees. Of the stimuli to which these responses are made he writes: "An essential feature of the stimulating conditions is the divergence of the object avoided from a familiar group of objects while still having enough of their properties to fall within the same class" [305]. Such behavior may be widespread at least among the mammals, but much remains to be learned about its manifestations and intensity in different species. In unpublished work, P. E. Cowan finds *Rattus rattus*, like *R. norvegicus*, to be markedly neophobic. These commensal species have been compared with two Australian congeners, *R. fuscipes* and *R. villosissimus*, both largely independent of man and neither neophobic in the laboratory conditions in which they have been tested. The typical new object reaction, first clearly described in investigations of rats as pests, is perhaps a product of natural selection in man-made environments. But there is no universal rule: the commensal house mouse, *Mus musculus*, displays, instead of typical neophobia, a capricious and unpredictable kind of behavior [634].

3.4 THE ECOLOGY OF EXPLORATION AND AVOIDANCE

3.4.1 The Functions of Exploration

The discussion so far has been mainly on the stimuli which evoke approach or avoidance. We now turn to their survival value.

Wild rats, once they leave the nest, are subject to predation, and their principal means of avoiding predators are the use of pathways under cover, and flight to a burrow or other place of concealment. These actions depend on previous experience of the topography of their living space. Given such experience, they can run from any one point to any other, by the shortest route and in the least possible time. Rats are more vulnerable to predation by cats if they are in unfamiliar surroundings [219]. But exploration does not lead only to learning where cover and nest sites are: it is accompanied by sampling of the edible or potable materials encountered, and so a rat is regularly informed of sources of food and water. A further consequence of general movement is that odor trails are left on the routes regularly used, and these are detected by other rats (§§5.2.3; 8.2.4.1).

The word "random" is sometimes applied to exploratory behavior. A more appropriate term would be "unpredictable"; but even this is misleading. The direction of a rat's movements, even in an unknown terrain, is influenced in an orderly way by many of the features it encounters. The inorganic stimuli may be tactile, visual or olfactory. (The vibrissae, as Vincent [695] has shown, play an important part in receiving tactile stimuli.) A similar variety of stimuli may be provided by other rats.

Rats, like many other small mammals, tend to move in contact with a vertical surface; they also eat in a corner rather than in an open space. These are examples of thigmotaxis, or movement directed by tactile stimuli; they are among the few examples of specific orientations encountered in rat behavior. Thigmotaxis, formally studied in young rats by Crozier [181], has usually been regarded as behavior which appears regardless of the conditions in which the rat is reared or of any particular sort of experience. But Patrick & Laughlin raised rats in an environment without opaque walls, and they did not develop a tendency to move close to a wall [521]. Here is an example of difficulty in determining how a behavior pattern develops and to what extent it is independent of individual experience. (§9.2.2). Functionally, thigmotactic behavior is presumably an aspect of taking cover from predators. A more obvious example is the tendency, already mentioned, to move from light to dark. Other guiding stimuli are more likely to lead to exposure: the odors of food or of other rats have an attractive effect which may overcome the shelter-seeking tendency.

The explorations of rats in any ordinary environment have, then, superimposed on them, effects of external stimulation which make the direction of movement more predictable than it would be if it were influenced only by the novelty of the surrounding objects.

3.4.2 Avoidance Behavior

If wild rats in human communities behaved as tame ones do toward unfamiliar objects, their compulsive exploratory and sampling behavior would probably lead them into traps or result in the ingestion of poison bait. Neophobia, displayed in a highly developed form by wild rats, protects them from the consequences of curiosity. The extent to which rats commensal with man display avoidance behavior is perhaps a consequence of selection over the seven thousand years during which civilization, with its stores of food, has existed. More intense selection *against* wildness and neophobia produced the laboratory rat in less than half a century.

Avoidance of strange objects, and especially strange animals of the same and other species, is common in the animal kingdom. It develops early in the life of many species of birds and mammals after a brief period when the young become imprinted (§8.7.2.1) on their parents. Once this young-parent attachment has been acquired, the safety of the young is well served by their avoidance of other animals. The avoidance behavior of wild rats may have a source in this kind of behavior, but on such questions one can only guess.

Whatever its evolutionary origin, the neophobia of wild rats is not by itself sufficient protection against poisoned food. It is combined with a capacity to learn to refuse toxic mixtures. This capacity parallels the ability, much studied in tame rats, to select, in some instances, the nutritionally superior of two foods (§4.3.1.2). The combination of exploring and avoidance with habit formation is therefore elegantly adapted to giving a rat a maximum of information about the resources and dangers of its environment, in the safest possible way.

3.5 DEFINITIONS

Many animals regularly explore their surroundings: that is, they approach and enter every accessible place in an area or volume around a nest or resting site. Sometimes such movements end when a specific ("consummatory") state is achieved, whether by performance of a "consummatory act" or not; or, if movement does not cease, a new kind of activity follows. It is often possible to say, or to infer, that the activity has been evoked by a specific internal state, such as a food deficit, or an adverse external feature, such as cold. The term "appetitive" is sometimes applied to such behavior, and is then often used to distinguish variable (unpredictable) movements from stereotyped activities such as courtship ceremonies; the latter are fixed (predictable in detail) within each species. But the behavior called appetitive may include quite standardized movements, such as those of an animal with a well-fixed habit of moving from its nest to a food source; the movements are then predictable for that animal, at least while its environment remains unchanged. By contrast, some movements are unrelated to any goal and, probably, independent of any special internal state. The movements of satiated rats in their living space are variable movements which we cannot relate to any immediate need. They are seen most readily among laboratory rats, but wild rats are also highly exploratory. The movements are not a spontaneous motor activity but are a result of a general tendency to vary the stimulus situation. Other species, from cockroaches to man, behave in a similar way.

When, therefore, a rat walks, runs or clambers about, the activity may be impelled by a deficit or it may be evoked by the novelty of the surroundings; or there may be some component of each influence. Except in special experimental situations, it is not possible to make quantitative statements about the contributions of the different factors to the level of activity. Hence it is hardly appropriate to divide the ranging movements of rats or other animals into "appetitive" and "exploratory": in this book, the term "appetitive" is therefore not used except in reference to the writings of others; and "exploring" refers to behavior which diversifies the input through the senses.

The recent analysis of the causes of activity has made a major contribution to the theories of behavior. It has also substantially improved our understanding of the lives of a number of species, especially *Rattus norvegicus.* Wild rats, given access to an unfamiliar area, explore it. They also regularly re-explore their home range. Such activity provides information about the resources and dangers of the environment. (The storage of information that occurs when an animal explores is further discussed in § 8.2.2.) But movement in a familiar area is inhibited by the presence of an unfamiliar object or arrangement. Neophobia is hardly displayed by laboratory rats. It protects wild rats from danger: these animals possess a delicately balanced and highly efficient combination of movements of approach and avoidance, which often enables them safely to make the most of what the environment has to offer.

4 Feeding Behavior

Not one man in a billion, when taking his dinner, ever thinks of utility. He eats because the food tastes good and makes him want more. If you ask him why *he should want to eat more of what tastes like that, instead of revering you as a philosopher he will probably laugh at you for a fool.*

William James

4.1 GENERAL

Much of the behavior described in the preceding chapter is only indirectly related to the primary needs—those that must be satisfied if the animal is to survive for more than a few minutes, hours or days. The internal processes which determine that animals behave so as to satisfy these needs are sometimes called the homeostatic drives. They are set in motion by a departure from some internal state, such as the concentration of sodium ion in the body fluids, the amount of carbon dioxide in the blood or the temperature of the skin: for each of these there is a narrow range of values which a mammal tends to maintain.

This chapter deals with the activities which maintain a rat's intake of food and water. The feeding of most animals is regulated by complex mechanisms; but in studying an omnivorous mammal we are taking on the most difficult of the possible tasks. Omnivory, however, is not special to the genus, *Rattus*, or even to the family Muridae. Although the rodents are specialized, in their dentition and in head structure, for eating hard plant food, such as grains, many of those that have been studied closely have proved to be versatile feeders. The voles of the genus, *Microtus*, feed principally on the softer parts of rough grasses; but they readily take to roots, such as carrots or turnips; and they also eat grain [218, 536]. *Apodemus* and *Clethrionomys*, too, are adaptable feeders [266]. Squirrels (Sciuridae) eat hard fruits and seeds, but also young shoots and buds, young bark, roots and even insects [607]. Gerbils, such as *Meriones*, may eat a high proportion of insects, instead of plant foods, at certain seasons [529]. Some species of *Rattus* eat land snails [415]. In some conditions half the diet may be insects, especially termites [297]. Rats can also be predators on smaller mammals, birds and even fish. The factors which regulate feeding in natural conditions are almost unknown. Since we are principally concerned with the results of experimental analysis, we are obliged in this chapter to rely almost entirely on observations of laboratory rats.

4.2 THE COMPONENTS OF FEEDING BEHAVIOR

4.2.1 Directional Movements

4.2.1.1 *Olfactory stimuli.* The variable movements of rats tend to put them regularly in every accessible spot in a substantial area around their nest. This enables them to discover food and water, and to take advantage of new sources as they appear. The variable movements are supported by the sampling of all materials encountered. The stimuli involved are largely olfactory and gustatory. The olfactory sense of a rat, as of most other mammals, plays an important part in behavior. The structure of the brain reflects this olfactory dominance (figure 4). Probably, odor leads to the first sampling: any of a wide range of odors seems to induce licking, and this is usually followed by actual eating.

The effect of odors in attracting laboratory rats has been studied by Neuhaus. A rat continually sniffs and turns its head; there must consequently be rapid variation in the intensity and character of the stimuli influencing the olfactory organs (yet a further aspect, perhaps, of the tendency to vary the sensory input as much as possible). The direction of the movements of rats is influenced by air currents which carry odors. Neuhaus put rats where they had a choice of two tunnels, with air currents bearing different odors, and trained them to go to food marked by the odor of formic acid; after this the rats continued to do so when given a choice between the odor of formic acid and another, such as acetic or valerianic. But rats trained to approach formic acid, and given a choice between this and butyric acid, went to the latter, and had to learn *not* to do so. In these experiments butyric acid acted as a lure [498]. (For wild rats, by contrast, butyric acid is a deterrent [61].)

Eayrs & Moulton have made a more thorough study of the olfactory acuity of laboratory rats. In determining the direction of movement, odors are subordinate to other sensory cues: the olfactory stimulus should be close to the reward (for instance, food) if learning to respond to the stimulus is to be efficient [211].

These experiments suggest three conclusions. First, odors can determine the direction of a rat's movements. Second, there are probably species-characteristic responses (approach or avoidance) to some odors; this supposition, however, needs to be tested: we know rather little about the more subtle effects of experience, especially early experience, on choice of odors or flavors. Third, rats can learn to associate food with particular odors, and even with an odor from which they have previously shown an aversion.

4.2.1.2 *Social stimuli.* The direction of a wild rat's movements as it goes to eat may also be influenced by other rats. In this book the word "social" is used for any such effect.

Barnett & Spencer watched colonies of wild rats when they began to feed in the evening. The food was wheat grains. Usually, one particular member of the colony emerged first, and carried a mouthful of grains back to its nest; the nest was shared with other rats, and these came out soon after the return of the pioneer rat. The possible importance of such individuals appeared in two kinds of situation. In one, the rats were deprived of food for one or two days, and then food was replaced in the usual containers. The first rat to find the food was the pioneer, and the return of this rat to the nest with food led to a rapid and unanimous sortie by the rest of the colony. This occurred, as one would expect, especially when the rats had had previous experience of a fast followed by a return of food. In a second kind of experiment, food, for instance cabbage, put in the enclosure was of a kind only rarely available to the rats. The first rat to emerge at once took a cabbage leaf and returned with it to the nest. This was followed by general activity, including excursions for additional leaves and attempts to wrest fragments of leaf from other rats.

The habit of taking food to the nest, and of eating it under cover, had other indirect social effects. Grains dropped from a rat's mouth, as a preliminary to eating them one by one, were often taken by other rats. If a rat had been eating flour, residues on its face or hands were licked off by other rats, especially young ones [60]. Chitty [151] has seen young rats, on coming back to cover with a mouth full of grains, turned on their backs and robbed by older rats. Theft never led to conflict. The rats had probably come to associate certain behavior of other rats, or certain appearances or odors, with the presence of food. The fact that a social interaction is involved is incidental.

It is often suggested, nevertheless, that rats are co-operative animals, and band together to carry food to their nests. There is a persistent legend that eggs are taken in the hands of one rat which then lies on its back while a second rat drags it by the tail to cover. This belief should not be casually dismissed: rats do use their hands for grasping, and they do pull each others' tails. It is not impossible that rats could learn, almost accidentally, to perform some such trick. But the only authentic account of egg-stealing by rats with supporting photographs (plate 6) shows the rats operating individually: each pushes an egg along in front of it. Similarly, when rats, in the colonies mentioned above, found a lump of liver weighing 450 g outside the nest, the larger ones dragged it under cover (plate 5). Sometimes two or three were seen heaving away at one time; but they did not pull in the same direction: on the contrary, they often pulled in opposition [60].

It is possible in rather special conditions to induce laboratory rats to adopt a form of co-operation. Mowrer has described experiments in which three rats were put in a modified Skinner box (compare plate 24); pressing a lever at one end of the cage released food at the other. At first no rat did much lever-pressing, evidently because doing so led to no reward for the performer but only an unearned pellet of food for one of the others. Eventually, however, *one* of the rats developed the habit of doing enough work to satisfy the needs of all three (figure 25). The apparent parallel to one kind of human community was in this case a result of the formation of a simple habit. An interesting question, still not answered, is what determines that one rat should become a worker and the others dependents.

There are other myths about co-operation by rats. Among them is the story of adults warning young rats of the dangers of poison bait. There is no valid evidence for this; but we are justified in asking whether there are social influences on the development of the feeding habits of young rats. Weanlings often follow their mother, but a female with active young does not, except incidentally, guide them to food. She may, indeed, push them out of the way if they obstruct her while she is eating [36]. Young rats may also follow other adults. The importance of this behavior is discussed below (§ 4.3.3).

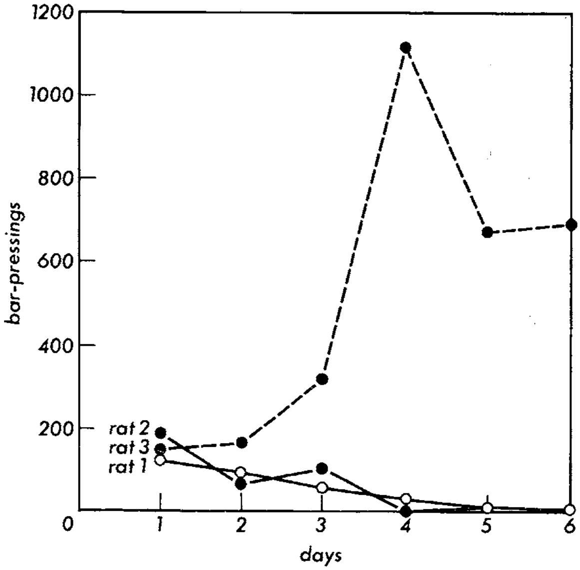


Figure 25. "Co-operative" behavior. Three laboratory rats were put in a cage (a Skinner box) in which pressing a bar at one end released food at the other; there was no other source of food. For two days little bar-pressing was done; but, after this, one rat developed the habit of working for all three. (After Mowrer [486].)

The social effects on feeding, then, reflect the ability of rats to develop habits in response to all kinds of stimuli, including those provided by other rats; but no other social interactions are involved, except, of course, those of a mother with sucklings.

4.2.2 Avoidance and Its Aftermath

The preceding paragraphs are concerned with the approach to food. But wild rats, although they eventually sample everything within range, at first avoid an unfamiliar food, or a familiar food in a new place (§ 3.3). There are three aspects of the effect of neophobia on food consumption. First, an environmental change may cause an interruption in feeding, even though the food is not changed or moved (figure 24). Second, a change in the conditions at a feeding point may reduce the amount eaten at that point, without influencing eating elsewhere. Third, a new food can itself induce at least a transient avoidance; this must be distinguished from the avoidance developed as a result of eating a toxic food (§ 4.3.1.2).

Neophobia wanes, as a rule, quite rapidly. If a new food becomes available, increasing amounts are eaten, until it may even be preferred to what was eaten before (figure 24). When the amount of food is less than the rats can eat, a further effect is observed: as neophobia is overcome, the time of eating may change also. Thompson studied rats living in natural conditions; some had been caught, individually marked and released. Figure 26 shows the progressive concentration of feeding near the time when food was made available each evening; in these conditions, the intensity of feeding is increased, and its duration reduced: the behavior is adapted, not only to place, but also to time.

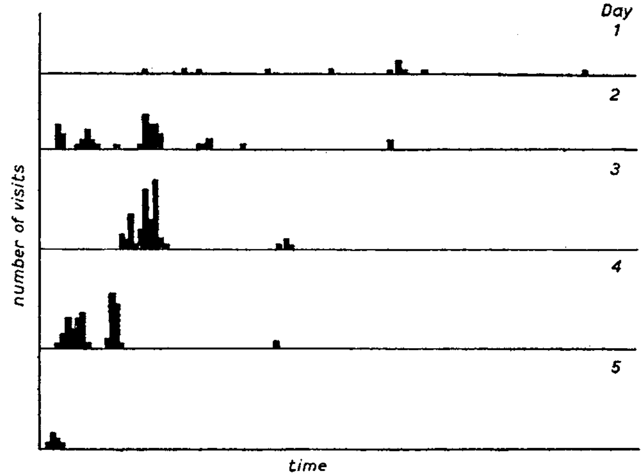


Figure 26. Decline of avoidance of unfamiliar food with time. Each histogram records the number of visits of a single marked wild rat, living in a colony on a pig farm, to a pile of food. The record for each day begins at 17.00 h when the food was put down. Food had not been available at this place before the first day of the experiment. On the fifth day poison was added to the food and this rat, together with most of the others, was killed. (From Thompson [672].)

4.2.3 Eating

Eating involves licking, chewing (or gnawing), salivation, swallowing and handling. The first is an important part of sampling. Salivation and swallowing are usually called "reflex" activities, and are therefore often disregarded by students of behavior. Gnawing and handling may be discussed more fully.

Gnawing is the eponymous characteristic of rodents, but it has been surprisingly little studied. Wild rats gnaw structures such as lead pipes for no evident reason [47]; in this way they often do much damage without benefiting themselves in any obvious way. Even laboratory rats may chew bits of wood if given the opportunity [358]. Wild house mice, *Mus musculus*, indulge in apparently functionless gnawing more than laboratory mice [621], and hybrid laboratory mice more than inbred [57]. The behavior is evidently not a peculiarity of domestic varieties, or of life in laboratories. Rats are neophilic in their choice of what to gnaw: they select unfamiliar rather than familiar objects.

Neurological findings confirm that gnawing is not necessarily linked to eating. W. W. Roberts & Carey stimulated the mediolateral hypothalamus of laboratory rats, and induced the animals to gnaw fragments of wood or cardboard. If, during such stimulation, objects which could be gnawed were put at the end of one arm of a **Y**-maze, the rats learned to go there: the objects constituted a reward. The experimental animals did not gnaw objects unless they were stimulated; controls were stimulated in other parts of the brain, and did not gnaw at any time. The most remarkable observations were made when stimulation was turned on while the animals were eating food powder: they stopped eating and turned to gnawing whatever objects were available. Gnawing induced in this way by central stimulation was independent of the nutritional state of the animals [550].

Manipulation is another feature of the behavior of all rats. Wild rat nestlings handle objects as early as thirteen days, before the eyes open: they may take fragments of wood in their hands and, in a clumsy manner, convey them to the mouth [47]. Newly weaned wild rats have also been watched feeding for the first time on flour or sugar: they begin by burying their noses in the food but, as a rule, within a few minutes they use one or both hands, at first intermittently but soon consistently. For some weeks, nevertheless, young rats, like babies, continue to spill a good deal of food, and they only gradually come to feed with little waste [36].

Among adults, although handling always occurs, there is much individual variation. Typically, a rat rests on its hind quarters and uses both hands (figure 27). Spencer has described how the stereotyped nature of this behavior even extends to the precise way in which a cereal grain is nibbled: smaller rodents, such as house mice, hold a grain at right angles to the long axis of the body, as a man eats corn on the cob, but a rat holds it as a man holds a cigar [636]. This may be due to learning which is the more convenient way of eating grain: the difference between mice and rats may be merely a function of size. Certainly, if one watches wild rats eating flour, one sees no uniformity in the detail of the movements: one may squat and use two hands in the manner described; another may put its nose well down into the food (plate 7); a third may sit up and use one hand as a scoop.

Although, then, handling is a characteristic of all rats, its details vary among individuals; and we cannot at present identify the factors involved in its development. No doubt there are features in the structure of the limbs, and in the workings of the central nervous system, which are present in all rats and which enable them to use their hands; but the extent to which individual experience plays a part, and the exact nature of the relevant stimuli, have still to be discovered.

4.2.4 Carrying and Hoarding

Rats not only resort to their nests or burrows for cover and sleep: they also carry objects to them. The objects include straying young, and material for nest-building, as well as food. Stones, cakes of soap, bits of wood and much else may be accumulated in the same way [47]. We have no explanation of the storage of apparently useless objects, and it has been largely ignored in experimental studies of hoarding. Here we are concerned with carrying and hoarding as an aspect of feeding. When rats have made their way to food, they may take the food under cover before eating it (plate 5). They may do this even when they have been deprived of food for some time. Wheat grains are taken away in mouthfuls: even a rat of medium weight (250 g) can take six to eight grains at a journey; a large rat takes more, and may be seen shoveling them rapidly into its mouth until the cheeks are full [60]. Under cover, the grains are disgorged and eaten one at a time. Such behavior no doubt helps to protect rats from predators.

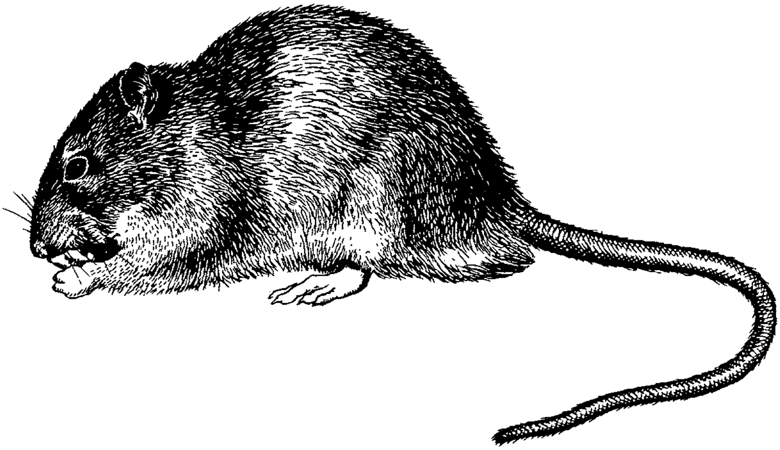


Figure 27. Adult, male *Rattus norvegicus* eating food held in the hands.

Sometimes food is taken to a nest or burrow and deposited without being eaten. In stable colonies of wild rats kept in large cages (§ 5.3), food cubes are sometimes removed as soon as they are put in the food boxes, and scattered on the floor or taken to the nest boxes [37]. This type of behavior is seen in an extreme form in natural, commensal populations of *Bandicota bengalensis*, studied by Parrack [519], Roy [563] and Spillett [637]. In an experiment by Parrack, these mole or bandicoot rats accumulated stores four times the weight of grain eaten in the same period. In paddy fields in the south of India, the amount of rice hoarded in the burrows is so great that it is dug out at harvest time and eaten by men employed to catch the rats. The rats, too, are eaten. Unfortunately, this economic measure does not compensate for the enormous losses due to this species. (The phenomena of hoarding have some curious implications for the relationship of rat numbers to food losses: clearly, even if, improbably, the size of a population were accurately known, losses could not simply be reckoned by multiplying this number by the mean consumption per rat.)

Calhoun has suggested another function for hoarding, from observations on wild *R. norvegicus* in a large enclosure: most of the rats stored food in their burrows, but especially those that had been mildly attacked by others; rats that had been severely attacked took food to scattered points nearby and then paid no further attention to it. Calhoun suggests that nevertheless the behavior has a function, since scattering food makes it more easily accessible to rats living at a distance from the main source [124]. If so, scattering would favor the growth of a colony by reducing conflict. But we still do not know just what induces rats to behave in this way.

Laboratory rats, too, hoard food, and hoarding has been the subject of many experiments, of which the early ones have been reviewed by Munn [490]. Tame rats, given objects such as food cubes in an open container, may at once pick them up and scatter them around the cage. In a cage with a covered refuge they tend to accumulate objects in this home, especially if the rats have recently been deprived of food for a time [479]. Such hoarding is not a direct result of hunger: it does not begin as soon as the rat is hungry, and it goes on long after the rat has been able to eat its fill—sometimes even for twelve weeks; and the pellets are typically not eaten but merely deposited in the living cage [478]. The adaptive significance of the behavior may once again easily be surmised; but even if we knew for certain that hoarding had survival value, either for the individual or for the colony, the *immediate stimuli* which influence it would still be open to study.

Collection of pellets suggests that their presence is the goal of the behavior; that is, removal of the pellets as they are deposited should increase the number brought in while, presumably, stocking the home cage ought to inhibit the behavior. The result of removing pellets as they are brought in varies [439, 440]: if the rats are not fasted, hoarding occurs whether the cubes are removed or not; but if they have fasted, removal of the cubes during preliminary training in the cage leads to an appreciable *reduction* in the number of cubes hoarded in a given time, when this is subsequently tested. The inhibitory effect of removal of pellets depends, then, on the extent to which the rat needs food at the time when it first experiences the hoarding situation. "Disappointment" at this stage leads to subsequent decline in the impulse to carry out an act which has proved fruitless on previous occasions.

Since rats are liable to take any portable objects to their nests, it may be asked whether they would hoard just as much if the pellets were not edible. Just as previous food deprivation may increase food hoarding, so previous water deprivation may increase the hoarding of water. This was shown by G. Miller & Vieck, who supplied pledgets soaked in water, instead of, or in addition to, food pellets. Given a choice, food-deprived rats chose pellets, and water-deprived rats took pledgets. Small wood blocks, offered as a further control, were taken little or not at all. The same authors investigated the characteristics of a home cage that induce rats to hoard there rather than elsewhere. Familiarity was found to be important, especially familiarity of odor [458, 694]. Another factor is the cover provided. Accumulation of pellets in the living cage is increased if the alley leading to the food tin is open, instead of closed at the top. Bindra observed greater hesitation in entering open alleys, and interprets his findings in terms of the greater "security" offered by the home cage [93]. This notion requires further analysis; it seems to confuse the adaptive significance (or selective advantage) of the behavior with the immediate stimuli that evoke it. But the importance of a home in which the rat is out of sight of enemies, has contact stimuli from the walls, is protected from drafts and bright lights and is surrounded by familiar conditions and odors, is very evident.

Hoarding by rats is, then, a complex activity analogous to the accumulation of food stores by squirrels (Sciuridae) and beavers (Castoridae). This has led to the use of the term "the hoarding instinct" [478]. If this expression is intended only as a name for a commonly observed activity, there is no great objection to it; but if it is intended to convey that the behavior is "innate"; or that it is universal among rats; or that it develops independently of a rat's individual experience; then it is misleading. This is well shown in a critical analysis by Marx [438]. Rats used in the experiments described above had usually encountered food pellets, and may have been influenced by that experience. Further, an understanding of the development of hoarding by an individual rat requires one to consider the several, partly separate, elements which make up the whole pattern. First, there is exploration; second, there is the homing or taking cover emphasized in Bindra's work cited above; third, there is the series of actions evoked by the pellet: seizing it (a preliminary to eating); carrying it to cover; and releasing it (before taking it in the hands to eat). The total pattern of hoarding includes all these components, of which each is held to be an independently acquired habit. This attempt at detailed analysis of a complex stereotyped pattern shows how involved the interaction between nature and nurture must be in the development of such an activity (§ 11.4).

4.3 FACTORS INFLUENCING CHOICE OF FOOD

4.3.1 Physiological Effects of Food

4.3.1.1 *Favorable effects.* We turn next to the question of choice of foods. Two relevant facts have already been mentioned: first, rats which have experienced thirst hoard water rather than food, and food-deprived rats hoard food rather than water; second, if rats, wild or tame, have access to two or more foods, they do not ordinarily restrict themselves only to one, but at least sample all of them. In these ways exploration and the capacity to store information combine to enable rats to make the best use of what is available around them.

The versatility of rats in their food habits has obviously contributed to their success. It also makes them convenient animals for the study of food selection. Since they sample everything, their preferences must be expressed in terms of the proportion of different foods making the whole diet: among a wide range of foods, choice is a quantitative affair. This raises the question of the units in which the quantities should be expressed. Sometimes it is convenient to give calorigenic values, for rats, like other animals, regulate their eating so that energy intake balances energy output.

The constancy of energy intake in an unchanging environment is the most obvious example of the influence of physiological effects of food on eating: the amount of a food eaten depends, other things equal, on its energy value and that of other foods taken during the same period. Hausmann added ethyl alcohol to the drinking water of rats: the intake of other energy sources declined in proportion to the calorigenic value of the alcohol consumed. He also compared the effects of adding sugar or saccharin to the drinking water: the saccharin had (for man) the same sweetening effect as the sugar, but no energy value; intake of solids declined proportionally when sugar was added, but was unchanged with saccharin [301]. Similarly, when Adolph added indigestible "roughage" to food, the volume of food ingested increased so that its energy value remained constant; only when the proportion of nutrients in the mixture was reduced to one-third or less was the intake too little to maintain body weight. When food and water were given together, in the form of milk, the volume drunk was determined by energy needs alone, despite the excess of liquid that had to be taken [11].

The ability to regulate energy intake is not, of course a peculiarity of laboratory rats. Maller describes experiments in which trapped wild rats were given first a diet containing 10 percent oil, and then one with 60 percent. Intake was rapidly adjusted to the increased energy value of the mixture. Laboratory rats similarly treated also ate less, but took longer to adapt [431].

Energy intake is independent of the growth-giving quality of food, notably its protein content. How then is adequate protein intake ensured? Aschkenasy-Lelu [26], and E. M. Scott & Quint [589], studied the effects of protein deficiency on albino rats: given a choice between a low-protein and a high-protein diet, the rats did not adjust their intake to need; some ate enough protein, others did not, and it seemed impossible to predict which would happen. On this evidence, growth is an incidental consequence of consuming food that yields a specific amount of energy; but Maller has given evidence that wild rats can select a protein-adequate diet after protein deficiency has been induced [431].

Certainly, the nutritional value of individual substances can influence food choice. Early studies of "dietary self-selection" have been reviewed by Aschkenazy-Lelu [27] and later findings by Lât [396]. There is evidence of an ability to distinguish between solutions of amino-acids of different composition: Halstead & Gallagher offered a choice between a complete mixture and one without one of the essential amino-acids, threonine. There was much individual variation, but a strong tendency to select the complete mixture [285].

The earliest important study of self-selection was by L. J. Harris and his colleagues. They were primarily concerned with the physiology of nutrition, but were faced with the fact that what an animal (or a man) eats is not only a matter of food chemistry, but depends also on factors which may be unrelated to biochemical need; they were therefore led into observations of behavior and into asking what was meant when an animal's choice of diet was said to be due to instinct. They made rats deficient in vitamin B_1 (thiamin), and gave them a choice between two diets of which one was flavored with Bovril, the other with Marmite; the latter, a yeast extract, contains B vitamins. Control rats (not deficient) ate the diets without discrimination, switching readily from one to the other, unless and until they developed a deficiency; the deficient rats consistently ate the mixture containing B vitamins. If a choice of several foods was offered, the rats sometimes failed to identify the favorable one; but those that had previously experienced the "correct" mixture ate it even when presented with a large choice. Rats familiar with the choice situation "give a cursory sniff at each food in turn and then proceed to eat the vitamin-containing diet." The effect of thiamin on the heart rate was detectable an hour after its ingestion, and Harris and his colleagues attributed the correct choice of diet to association between this favorable physiological action and eating a particular mixture [295].

The importance of labeling diets with a distinctive flavor has been confirmed by Zahorik & Maier. They gave three kinds of flavored water to rats after twenty-one days of feeding on a thiamin-deficient diet. The rats sampled all the flavors. Whenever water containing one particular flavor was taken, thiamin was injected into a muscle. This reward was given four times. Thereafter, the rats preferred the taste which had been paired with the injections. The preference persisted even when the animals had recovered completely from the deficiency [735].

E. M. Scott and his colleagues made albino rats deficient in thiamin, riboflavin or pyridoxin; such rats chose a mixture containing the vitamin they needed, in preference to a deficient diet, even when the mixtures were not labeled with flavors [588]. Thiamin-deficient rats were not infallible in these conditions, but those that did succeed readily picked out the one vitamin-containing diet from four offered [591]. Tribe & Gordon, in carefully designed experiments, have even revealed a slight tendency to prefer a thiamin-containing diet among rats which are not thiamin-deficient [684].

The behavior involved in thiamin preference has been analyzed in some detail. Rodgers describes how thiamin-deficient rats tend initially to select novel diets, when well-nourished animals will eat mainly familiar foods [552]. This increases the probability that a food with plenty of thiamin will be sampled. Rozin has made detailed observations on the sampling behavior of thiamin-deficient rats, and the way in which it engenders the habit of eating mainly the most favorable of a number of foods [567]. This is an aspect of the exploratory behavior discussed in the previous chapter. Rozin has also brought evidence of aversion from deficient diets. In his experiments aversion was indicated by (i) a tendency to spill the food instead of eating it in a tidy way; (ii) chewing of other objects in the presence of the deficient diet; and (iii) rejection of the familiar deficient diet after recovery [565]. Rozin has also confirmed that previous experience of thiamin deficiency leads to a lasting preference for a thiamin-containing diet, even when the deficiency has long been made up [564].

Not all vitamin deficiencies are similarly met by altered preference: P. T. Young & Wittenborn, for instance, could not detect any self-selection by rats which needed vitamins A or D [732]. These substances have a slower physiological action than have the other vitamins [586].

The self-selection of B vitamins is paralleled by findings on the selection of inorganic salts, of which sodium chloride has been most studied. Adrenalectomized rats, given a choice of plain or salty water, consume a higher proportion of the latter than do control animals; they may consequently survive in good health [545]. They are sometimes described as consuming more salty water; but, as Peters has shown, normal rats, given a choice, drink two or three times as much 0.9 per cent saline as distilled water; and adrenalectomy leads to a lower consumption of distilled water, not to an increased intake of the sodium chloride solution [523]. Moreover, E. M. Scott and his colleagues made rats salt-deficient merely by feeding them on an almost salt-free diet, and observed no corresponding change of behavior toward solutions containing salt. Such rats do not need as much salt as those without adrenals; they may have taken enough to counteract the deficiency without showing any significant *preference* [592].

Another example of dietary self-selection is displayed after parathyroidectomy. The operation greatly increases the need for calcium, and gives rats an increased appetite for calcium lactate [545, 593]. Calcium-deficient rats, like those short of thiamin, tend to select novel foods [552].

There is scattered evidence, reviewed by Lepkovsky [409], on the selection of advantageous diets by other mammals, including man. The phenomenon is probably a general one.

4.3.1.2 *Unfavorable effects.* A necessary counterpart of food preference is at least the partial rejection of a second food. Consequently, it may sometimes be unclear whether the favorable effect of a selected food, or the unfavorable action of the food rejected, is significant. The work of Rozin on thiamin-deficient rats, mentioned above, illustrates this. Figure 30 gives an example which also introduces the complexity of preferred flavor (§ 4.3.2). In experiments, the more nourishing of two foods is commonly assumed to have an internal effect which gives it reward-value, in the sense in which that term is used in studies of habit formation (§ 8.3.1.1). In accord with this assumption, less nourishing foods are accepted if no better alternative is offered: there is no evidence of an aversion from these foods. But rats made hungry will accept flavored food which, when offered with an unflavored alternative, is completely rejected [61]; hence failure to reject a food is not complete evidence of its general acceptability.

There are, as already mentioned, clear instances of acquired rejections in the effects of poisons on wild rats. Wild rats avoid new things, including foods, in a familiar environment. Chitty and his colleagues found a stage of total avoidance of bait, followed by a tendency to sample it: gradually, small amounts of the food are taken. It is as if "fear" and "curiosity" are in conflict, the first gradually declining and giving way to the second; yet a single act of sampling seems to result in a temporary decline in "curiosity" (or an increase of "fear"), since it is typically followed by a period in which the food is not eaten [151, 154, 572].

The interval after the first sampling gives an opportunity for the substances eaten to act on the body. If a poison is present, it may begin to take effect and, for a time, put an end to feeding altogether. If the rat recovers, as when little poison has been taken, it may then refuse the poisonous mixture on subsequent occasions [572]. This is evidently the obverse of the dietary self-selection described above: the rats have learned to reject instead of accept.

Probably, the rats' behavior toward the bait changes in other ways also. There are anecdotal accounts of several species, including *R. norvegicus*, covering baits, traps and miscellaneous objects with earth or other material. This odd activity seems not to have been recorded systematically for wild-type rodents, but Hudson has induced laboratory rats to display it. His rats were kept in groups, fasted and then fed at a point where there was a strip of plastic painted in black and white stripes. When they were feeding, they were given a slight shock. If, later, the striped pattern was again presented, without shock, the rats often covered it with the wood shavings supplied as bedding [336]. This observation seems not to have been followed up.

Chitty has described the results of a long series of experiments in the field, designed to reveal how many rats one kills by simply putting down poison bait at a large number of points in an infested area. The rat populations were estimated by a technique of indirect census; wheat grains were put down at many points, and daily consumption was recorded until a plateau was reached, as in figure 28; this gave a measure of the rat population. After poisoning, another census was carried out. Of fifty-eight experiments in which zinc phosphide, Zn_3P_2, or alphanaphthylthiourea were the poisons, only just over one-third gave an estimated reduction of 85 percent or over of the rat population; these figures illustrate the protective effect of avoiding new objects, sampling and learning to reject injurious foods [151].

The poisons used by Chitty and his colleagues were not among the most toxic available. Zinc phosphide has a LD_{50} of about 41 mg/kg body weight: that is, administration of this dosage to a large number of rats may be expected to kill half of them. Much more toxic poisons might be expected to kill more. Barnett & Spencer used sodium fluoroacetate, which has a LD_{50} of about 3.8 mg/kg for laboratory rats and is possibly still more toxic to wild rats. Even with this poison, there were failures. One consequence of unsuccessful poisoning, already mentioned, is a tendency of rats, after recovery, to refuse the food that has caused illness. This "bait-shyness" was found in colonies which had been subjected to sodium fluoroacetate, as well as to less drastic poisons [59].

We saw in § 3.4.2 how the combination of neophobia with exploratory behavior enables a wild rat to inform itself about its surroundings and yet avoid danger. The additional phenomena of food-sampling and food-refusal make wild rats exceedingly difficult to poison. Chitty and his colleagues overcame this difficulty by "pre-baiting" [154]. A palatable and nutritious food is placed in small amounts in the entrances of burrows or other places regularly visited by rats. This is repeated daily for (say) four days, by which time the rats have overcome their neophobia and are eating the food readily (figure 26). Poison is now added to the food; the rats eat it in toxic amounts, and die. (When the bait is put in the entrances to burrows, it is necessary to bait only on days 1 and 3, and poison on day 5.) This method, though laborious, is economically highly effective: casual poisoning, by contrast, at best merely reduces a population to a level at which its reproductive capacity is near the maximum (see § 5.3.1).

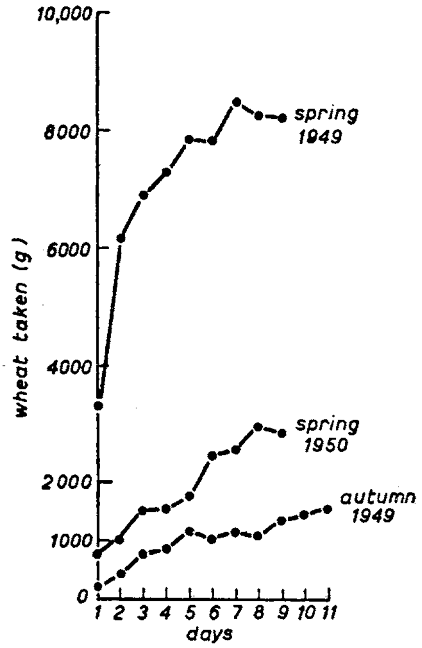


Figure 28. A method of census. Each graph shows the daily consumption of food by rats in a small English village. The amount eaten rises steadily to a plateau which provides an index of population size. After the first census, in spring 1949, a thorough poisoning campaign was carried out. The other two graphs represent the rat population level six months and one year later respectively. (After Barnett *et al.* [49].)

Prebaiting involves putting down only token quantities of bait, such as 60 g at each point. It should be clearly distinguished from census baiting (figure 28), which requires that a surplus should be laid at every convenient site.

The poisons so far mentioned act quickly, and this is no doubt a factor in the development of poison-shyness. It might be supposed that a poison with a slow action would take effect insidiously, and would not cause shyness. With such a poison it should be possible to dispense with pre-baiting. Accordingly, rat control has been attempted with poisons which act cumulatively, as a result of repeated ingestion over a period of days. One example, dicoumarin (3·3'-methylene-bis-4-hydroxycoumarin), gradually reduces the clotting power of the blood, and causes internal bleeding. Large populations of wild rats, given food mixed with dicoumarin, were substantially reduced, but the effect fell short of complete destruction: after some weeks, an equilibrium was reached between the lethal effects of the baiting and breeding by the rats (figure 29). This was attributed to the development of food-shyness, but may have been due to the presence in the population of a minority of individuals immune to the poison. Later, a slightly different anti-coagulant, 3(2-acetyl-1-phenylethyl)-4-hydroxycoumarin, ("Warfarin") was introduced. Surprisingly little rigorous research on the effects of this substance has been published, but it has certainly represented a major advance in pest control. Individual rats have evidently no behavioral riposte to it. Nevertheless, where this poison has been used intensively, rat *populations* have arisen on which it has little effect. They evidently represent the result of selection of genotypes which confer resistance [209].

Experiments in the field throw light on the ways in which behavior contributes to survival, and provide at least indirect evidence on the responses of rats to food; but they do not give conclusive evidence of phenomena such as bait-shyness. For instance, poisoning soon causes a *general* refusal of food; this is not bait-shyness, since the latter involves discriminating a food that has caused illness from others. General avoidance is, as Rzoska has shown, one feature of the behavior of rats that have eaten poisoned food. Moreover, in the field it is usually impracticable to study rats individually; and the survivors after a poisoning may be exceptional rats, not to be compared with those that have succumbed. Laboratory experiments have, however, also confirmed that rats do learn to refuse foods that have made them ill. Further, the rats' learned aversion may be displayed to only one component of a mixture which has previously had a toxic effect: if a bait containing sugar has poison added to it, and rats survive the poisoning, they may subsequently refuse other mixtures containing sugar. These facts apply both to wild rats and to albinos [24, 572]; and, as Prakash & Jain have shown, other rodents, such as gerbils (Gerbillidae), can develop poison-shyness [528].

The findings so far described in this section were made by ecologists concerned, in war-time, with problems of pest control. Psychologists have now begun more detailed analysis of the behavior (reviewed by McFarland [447]). There is perhaps a general lesson in this historical sequence: workers who intrude on a subject from another speciality may discern important features unnoticed by the experts.

Among some notable experimental analyses are those of Garcia and his colleagues. One procedure has been to administer a flavored mixture at the same time as a poison, but by a different route. Saccharin, for example, is given in drinking water, and shortly afterwards a sublethal quantity of a solution of lithium chloride, LiCl, is injected directly into the stomach, or intraperitoneally. The poison causes inactivity and loss of appetite. After one such event a laboratory rat refuses the saccharin solution, even if it is not offered again for several days. As we know, saccharin is not itself repellent. More-

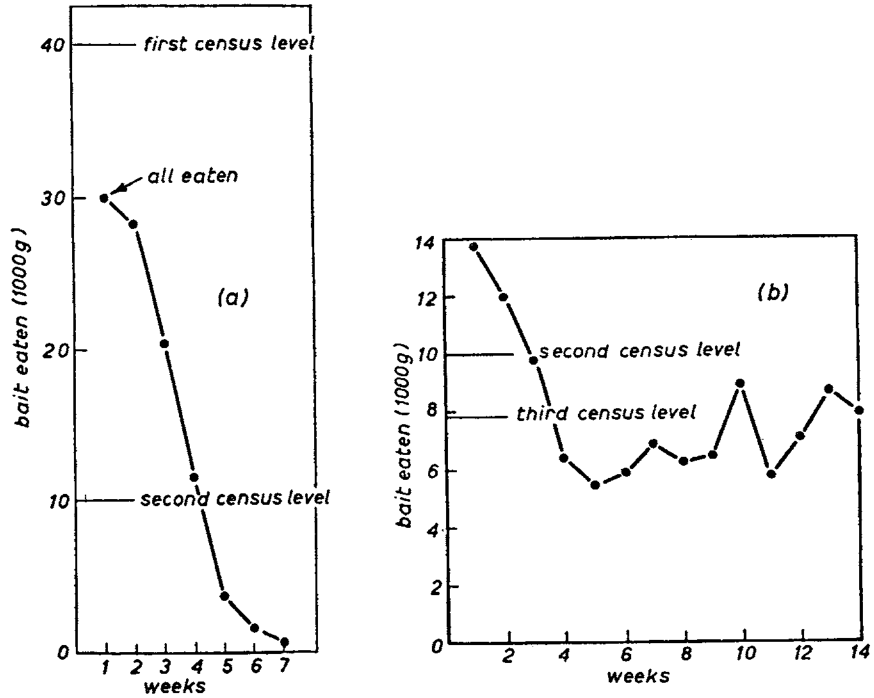


Figure 29. Effect of a cumulative poison. Graph (a) shows the weekly consumption, by a large colony of wild rats, of a bait containing dicoumarin, a blood anticoagulant which acts as a cumulative poison. Before the poison was first put down, a census indicated a population of at least 1,600 rats; the poisoning evidently reduced this number by about 75 percent. Graph (b) shows what happened when the residual population was given the same poison in a different bait base: there was little effect in fourteen weeks. Whether this was because the rats had developed poison shyness is uncertain; some may have been resistant to the poison. (After Armour & Barnett [24].)

over, the same sweet solution can be used in experiments which encourage rats to drink it: thiamin-deficient animals are given the solution, and then an injection of the vitamin which makes up the deficiency; they then increase their consumption of saccharin, just as if it were the solution that had cured them [250–52].

In experiments of this kind, the rôles of the taste and olfactory organs are not distinguished. Hankins and others made laboratory rats anosmic by direct treatment of the nasal mucosa with a solution of zinc sulphate, $ZnSO_4$. Anosmia did not interfere with the ability to develop a food-illness aversion. Hence, for this behavior, taste is presumably the important source of information. But olfactory bulbectomy, an operation often employed to induce anosmia, did interfere with the development of aversions. Evidently, the olfactory bulb (§ 2.3.1) is not merely an organ for reception of the olfactory input: it also has an integrating function. Odor alone can be made aversive, but only with prolonged training [287]. As we saw in § 3.3, the olfactory sense is more important in the response to novel stimuli.

The capacity of rats to develop food aversions has also been analyzed by exposing them to low doses of ionizing radiation. Garcia & Koelling [250] have reviewed this work, and Garcia and others [252] have described some unexpected findings from it. A single dose of 10 to 50 R, given when the subject is drinking flavored water, can induce an aversion from the flavor, although no avoidance occurs during irradiation. The same effect is observed if the animal is irradiated shortly before it drinks the water. By a similar procedure, an aversion from an odor may be induced; but aversions from a combination of visual, auditory and tactile stimuli require much higher doses. Similar differential effects are found with lithium chloride, and with a drug, apomorphine hydrochloride, which make some mammals vomit. These effects may be observed even if the illness develops several hours after consumption of the food. They are a notable exception to the rule that effective training requires a brief interval, preferably of seconds, between the conditional stimulus (in this case, the fluid) and the effect associated with it.

The use of radiation also allows a new approach to the chemical senses [250]. A given dose of radiation constitutes a precise, easily regulated aversive stimulus, which can be paired with the ingestion of any mixture that an experimental animal can be persuaded to take. It can also be paired with an odor.

It is a reasonable hypothesis that substances which have disagreeable effects on people are just those to which animals develop aversions. The use of radiation shows that food aversions can arise in a quite different way; and now Berger has described experiments which warn us against anthropomorphic assumptions in this field. He tested a number of drugs for their capacity to induce an aversion, by administering them shortly after rats had been allowed to drink milk. In these conditions, modest doses of a stimulant, amphetamine, chorpromazine (used clinically as a tranquilizer) or other therapeutic drugs led to aversions [86].

4.3.1.3 *Sampling and its significance.* The tendency of rats to sample whatever offers is necessary for the formation of favorable feeding habits, whether of positive preference or of aversion. It would be further advantageous if dietary deficiency increased sampling of novel foods (neophilia) and reduced readiness to eat the familiar diet which has led to deficiency. For the latter, Rozin has coined the term "paleophobia" [566]. Similarly, it would be appropriate if acutely poisoned rats became neophobic *in general* (as distinct from avoiding a particular food, that is, poison-shy); they should then become correspondingly paleophilic. There is evidence of all these effects [541]. Thiamin deficiency, for example, induces a change of behavior when rats, as in nature, have access to a number of possible foods. Each food is lightly sampled, and these snacks are taken at intervals of several hours. Any special physiological effect of one food then has time to become evident. Thus a rat can select a food, if one is present, that meets its needs.

There is evidence, moreover, that a mixture need not have a special physiological effect for it to influence food selection. Kalat & Rozin tested the hypothesis that mere ingestion of a food without subsequent ill effects increases its acceptability. They first showed that familiarity with solutions of sucrose or of casein hydrolysate, offered with tap water as an alternative, increases the readiness with which the solutions are drunk. Familiarity in this sense may be induced by only one experience of the solution. They then injected lithium chloride just after the rats had drunk solutions of sucrose, casein or sodium chloride. This, as we know, induces an aversion from the solution. But the degree of aversion was much reduced if the animals had, some hours before, ingested the solution with impunity. According to these authors, we have here a "learned safety mechanism": the animals in such a case learn, not that a solution is favorable or toxic, but that it is safe [351].

The changes in sampling and in size of meals described above must be distinguished from the development of particular food habits. Accordingly, adaptive feeding behavior may involve the following:

approach	*avoidance*
neophilia	neophobia
paleophilia	paleophobia
acquired preference	acquired aversion

The extent to which all these patterns of response contribute to survival in natural conditions has still to be discovered.

4.3.2 Palatability and Aversion

Choice of foods is not uniformly determined by homeostatic needs. Rats do not always perform like skilled dieticians. They may make their choice on an entirely different basis: their behavior then resembles that of a man who says he likes or dislikes some taste. The qualities of foods discussed in § 4.3.1 influence the amount of a food eaten by means of a change in the animal's behavior: the change, whether an increase or a decrease in the amount of food eaten, is due to a physiological effect of the food which can be objectively assessed as favorable or unfavorable. But some properties of foods induce either acceptance or refusal from the first, and continue to do so. There seems to be an organization of the chemical senses and the central nervous system independent of the differences of environment to which individuals are subjected; these features, in other words, appear to be very stable in development. This, however, is only a hypothesis, which needs to be tested by experiment.

Rats often prefer soft or finely divided foods to harder and coarser ones. Laboratory rats studied by Carlson & Hoelzel tended to eat the softer parts of grains and to leave the harder; but if grains were soaked in water, they were eaten whole [140]. Soaking, however, may influence taste, through the formation of sugars. The effect of texture is most clearly shown when two foods differ only in their state of division. Colonies of wild rats, observed by Barnett

& Spencer, preferred wheatmeal to whole wheat grains; since the meal had been made from the wheat, the state of division evidently determined choice. When one of these colonies, previously accustomed to eating whole wheat, was offered wheatmeal as an alternative, there was a gradual switch, lasting one to three days, before a steady intake was again attained (figure 30).

A similar effect is brought about by the presence in food of oils or fats. Albino rats have been studied by E. M. Scott & Verney [590], and wild rats by Barnett & Spencer [62]. Both eat mixtures of carbohydrate foods with oils of not very marked taste (for instance, arachis oil) in preference to the plain foods. Scott & Verney consider this to be an effect of palatability, not of nutritional value. Some other oils are refused, or eaten in only small amounts. Cod liver oil is accepted only in small quantities by wild rats, but this may be due to a toxic effect of the vitamin A it contains. Corn oil, cottonseed oil and butterfat are not eaten well by albino rats.

Figure 30. Effects of state of division and of sweetness on food choice by a colony of wild rats. Food was entirely refused for the first two days, because the food was offered in an unfamiliar container. On the third day whole wheat, which was familiar, was preferred; after that there was a change to meal, which is ordinarily preferred to whole grains by wild rats. Later observations showed the effects of adding (a) saccharin and (b) sugar to the meal. (After Barnett & Spencer [62].)

The effect of sweet flavor has been analyzed in detail; it illustrates the difficulties of interpreting preferences that at first seem simple. In colonies of wild rats, wheatmeal mixed with sugar is preferred to wheatmeal alone. Sugar of course has a rapid effect on an animal's internal state. But saccharin has a similar effect (figure 30), though observations by Gentile have revealed that saccharin sometimes repels laboratory rats [256]. These findings suggest that foods containing sugar or saccharin are preferred simply because of their taste, that is, for their direct action on the gustatory organs. Nevertheless, this conclusion, on the facts, could be regarded only as a hypothesis, for the following reasons. If rats have been accustomed to sweet foods (of which the maternal milk might be one), a sweet taste would be *associated* with food and its favorable internal effects, and so come to be the cue for a learned preference. In this case the sweet taste would be a secondary reward.

Sheffield and others, however, made laboratory rats discriminate between saccharin solution and plain water. The sweet taste was an effective reward in a **T**-maze in which turning one way enabled them to drink the sweetened water. The taste of saccharin was concluded not to be an acquired reward, for two reasons. First, the rats had not previously experienced anything so sweet and so, it was held, could not have learned to associate sweetness with a primary reward. Second, the effect of saccharin persisted, however long the rats were tested; whereas, if the saccharin were effective only through its association with some other action, such as that of food in the stomach, it would be expected to lose this effect with repeated presentations: that is, extinction of the response should take place [603–4]. This conclusion has not gone unchallenged. M. P. Smith & Capretta have more recently brought evidence that saccharin solutions act as rewards only when they have been associated with the presence of sugar in the stomach [626]. This contradiction has yet to be resolved.

The difficulties of studying apparently "inborn" features are referred to again in § 11.4, but one complicating factor may be mentioned here. As Collier & Bolles have shown, preference for sweet mixtures is influenced by the animal's nutritional state: if a rat has been fasted, its preference for foods with high concentrations of sucrose increases [162].

There are also flavors which, mixed with acceptable food, cause complete refusal if any alternative is available. Wild rats display such aversions more readily than laboratory rats. Scott & Quint, for instance, did not deter albinos by adding aniseed oil or butyric acid to their food [587], but Barnett & Spencer, in uncompleted work, found that both repelled wild rats. Barnett & Spencer used boxes with perforated zinc lids to test responses to offensive odors: the food was put on the lid of the box, and the odorous substance inside. A powerful odor, that of n-butyl-mercaptan, acted as a repellent: most of the rats fed from a similar box nearby that contained no odorous substance. Other stinks, less offensive to man, of substances which act as deterrents when actually mixed with food, gave less decisive results [61].

Much remains to be learned about the responses to tastes and odors. Among the problems is the extent to which apparently fixed responses can be modified by experience. Barnett gave young wild rats wheat mixed with cod liver oil or aniseed oil as their first solid food, with no alternative. Later, he offered the familiar mixture (which the rats had been eating regularly), and wheat mixed with arachis oil as an alternative; the young rats almost at once transferred their attention to the new, less noticeably flavored grains [36]. Evidently there are aversions which can be nullified by hunger, but there is no permanent alteration of behavior: given the opportunity, the rats turn to the usual choice. Nothing, however, has evidently been done yet to test whether still earlier experience, in the period when milk is the only food, can influence the preferences shown in later life.

4.3.3 Social Facilitation

The word "social" here refers to any behavior directly influenced by another member of the same species. We are now concerned with the circumstances in which rats stimulate other rats to feed or to eat more. Both come under the heading of "social facilitation"—a term defined by Crawford as "any increment of activity resulting from the presence of another member of the same species" [179]. Rats may seem to imitate other rats by feeding where the latter are already feeding. True imitation is rare in species other than man (§ 8.2.4.2), and apparently imitative feeding is an example of habit formation by trial and error (§ 7.3.4). Miller trained laboratory rats on a raised **T**-maze (figure 31) to turn toward either a white or a black card; the cards were on the right or the left, in a random sequence. A trained rat was put on the short arm of the apparatus, and behind it another rat; the second rat was rewarded with food, by raising the hinged lid of a sunken cup, if it followed (or "imitated") the first rat. In these conditions the second rat might be learning to respond to the card; control trials were therefore made without cards, and with the leading rat either untrained or trained to turn in a specific direction. Figure 31 gives some results. These observations illustrate how easy it would be, in more natural conditions, to mistake the results of ordinary habit formation for imitation. Since human beings imitate each other, we unthinkingly expect members of other species to do the same.

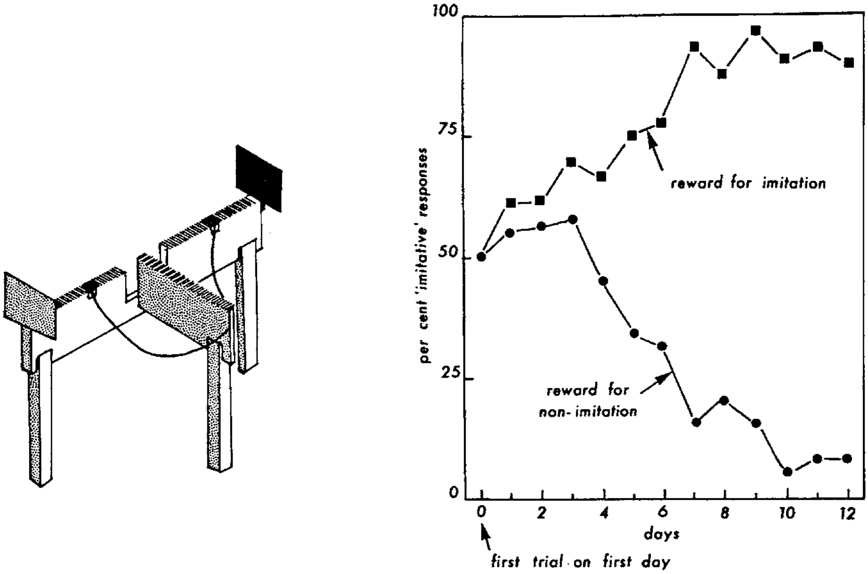


Figure 31. Imitation? Elevated **T**-maze used for studying a form of habit formation which resembles imitation. Two rats were started on the short arm. Reward could be given by opening a sunken cup, containing food, in one of the transverse arms. Some rats were rewarded for following ("imitating") the first rat, others for not doing so. The graphs show the result. (After N. E. Miller & Dollard [465].)

Another way in which social facilitation of feeding may come about has already been described in § 4.2.1.2, in the account of feeding in colonies of wild rats.

These examples of social facilitation may be accepted as results of straightforward training; but others are more obscure. Laboratory rats studied by Harlow ate more in groups than in isolation. The experiments were carefully controlled, and suggested that the extra eating resulted from a "competitive situation" [289].

Choice of food, too, may be influenced by the presence of other rats. The Soulairacs confirm that laboratory rats in groups of two or three eat more than solitary individuals; but if they are offered both a standard solid diet and a glucose solution, the rats in groups eat more of the former but drink less of the solution than the solitary ones; nevertheless, the net result is still a greater intake of calories for the grouped rats. Although the average increment was as great among paired rats as among those in groups of three, the increase among the former occurred only after about twenty days; but, when a third rat was added to a pair, there was an immediate increase in consumption, followed later by a smaller decline [632].

Interpretation of these observations is not yet possible, but they may be regarded as evidence of the peculiar effects of isolation (§ 5.4) as much as examples of social influences. The ill effects of isolation have been further illustrated by McDonald and others. Male rats were kept either in groups of twelve or alone. They were given a self-selection diet: sugar, a mixture of inorganic salts, protein (casein), and fat, in separate containers. The isolated animals grew less, evidently because they did not adapt themselves to this regime as well as those in groups [445].

It has often been stated, in anecdotes and moral tales, that adult rats guide their young to food, and even warn them of the dangers of poison bait. This is mere myth; but Galef & Clark have examined, in a series of experiments, a more general question. Are there any social interactions among wild rats which influence the development of food habits? They trained groups of wild rats to eat one food, and to avoid a second, by adding poison, in sublethal quantities, to the second. The rats were kept in small enclosures. When litters were born to rats so trained, the experimenter continued to offer the two foods, but neither contained poison. The adults nevertheless still displayed bait-shyness; and, when the young were old enough to forage, they too ate only the food that had not been associated with poison. Direct observation showed that the young rats persistently followed older ones, and this behavior seemed crucial in determining the feeding behavior of the young. Moreover, the habit so induced persisted even when the young were later separated from the adults. Similar experiments were carried out on laboratory rats; their young initially behaved like the wild rats, but after a few days they began to feed on the alternative diet. The difference is attributed to the neophobia displayed by wild, but not laboratory, rats [249]; but on this more work is needed.

None of these findings support the notion that rats have any complex cooperative social interactions, but they illustrate how much can be achieved without such behavior.

4.4 INTERNAL MECHANISMS

4.4.1 The Problems

In the rest of this chapter we are concerned with the internal mechanisms special to eating and drinking. The specific mechanisms are of two kinds. First, there are peripheral states, for instance in the stomach or in the composition of the blood. Second, parts of the nervous system are concerned in a very intimate way with eating and drinking: local damage to the brain may drastically alter, say, feeding, without having any other obvious effect. We then say that these parts "control" eating and drinking, though it is not easy to give any more precise meaning to this assertion, than to the statement already made: that damage to them deranges the behavior.

4.4.2 Water

Adolph and his colleagues [12] and Falk [231] have reviewed the factors which influence the intake of water by rats and rabbits. Adolph and others divide the process into four components: (i) seeking water; (ii) the act of drinking; (iii) stopping drinking; (iv) the absorption of water and its distribution to the tissues. Clearly, these could be further subdivided.

Seeking water is one aspect of exploration. An experiment by O'Kelly and his colleagues illustrates the adaptability of rats short of water in a completely bizarre situation. The rats were deprived of water for 23.5 hours and then given the opportunity to get water by pressing a bar. Some had to press the bar five times to get a sip, some ten times and some twenty times. Access to the bar lasted three hours. Before the bar pressing began, varying amounts of water or sodium chloride solution were injected directly into the stomach. The rate at which the bar was pressed corresponded precisely with the need for water [505].

Drinking occurs only if total body water is below a certain level, or if there is an excess of solute, such as sodium chloride, in the body. Water constitutes about 70 percent of the total weight of the body; intracellular water is about 50 percent, and contains as its principal cation, potassium; the main extracellular cation is sodium. Isotonicity between the cytoplasm of the cells and their surroundings (the *milieu intérieur*) is maintained by movement of water. There are probably osmoreceptors in the hypothalamus which respond to departures from osmotic balance: if there is too little water or too much sodium ion, the pituitary increases secretion of the antidiuretic hormone; at the same time, if water is available, the animal drinks.

There are probably several mechanisms which contribute to the final outcome of drinking in response to need. Kutscher has related drinking to cell dehydration: according to him, a one percent shrinkage in cell volume can lead to drinking [385]. The importance of the tonicity of body fluids has also been brought out by Hsiao & Trankina. They gave rats intraperitoneal injections of a salt solution isotonic with body fluids, and observed no consequent change in water intake; but injections of hypotonic solution in the same amounts led to a proportional decline in drinking [334]. Nevertheless, as Collier & Knarr have shown, a moderate water deficit, induced simply by reducing water supplies, is accompanied by decreased food consumption: this leads to a decline in body weight and the maintenance of a constant ratio of body water to lean body mass [164].

The preceding summary emphasizes the efficiency of rats (and other mammals) in adjusting their water intake to need. But if a rat is made hyperchloric, this condition is not followed at once either by copious drinking or a high rate of chloride excretion in the urine: there is no *rapid* compensation for an excess of solute in the body [12].

Work by McCleary has some bearing on this anomaly. He gave rats glucose and fructose solutions of varying strengths, after a period of water deprivation. Maximum intake was induced by a concentration of 5.3 percent, that is, at a concentration isotonic with body fluids. The lower intake of higher concentrations is attributed to their effect in the stomach: they cause withdrawal of fluid, and so bring about dehydration elsewhere in the body. This was tested by introducing solutions of glucose, saccharin or sodium chloride, of various tonicities, directly into the stomach. The effects of the treatment on subsequent drinking depended on the tonicity of the fluid injected. By contrast, intraperitoneal administration of glucose solutions did not lead to a reduced intake of glucose solution by the rats. This was held to be due to the different effect on the blood: intraperitoneal glucose does not provoke hypertonicity of the blood, but there is a lowered blood plasma volume. McCleary suggests that there are two kinds of thirst: in one, glucose is acceptable; in the other, it is not. The difference depends on the state of affairs in the stomach [444].

While the internal stimuli which provoke drinking are physico-chemical qualities of the body fluids, the cessation of drinking probably depends on receptors in the alimentary tract. Drinking can be stopped by distension of the stomach, either by filling it with fluid or by distending it with an inflatable balloon on the end of an esophageal tube [461]. N. E. Miller and his colleagues also gave water by stomach fistula to rats which had been deprived of water, and found, as had previous investigators, an immediately satiating effect: that is, the tendency of the rats to drink was reduced. But they found a still more satiating effect from the same amount of water taken by the mouth [466]. Evidently, receptors in the mouth or pharynx play a part in limiting the amount of fluid taken. The importance of mouth dryness—familiar to us subjectively—has been confirmed in work by Kissileff [372–4], in which two kinds of drinking are distinguished. Usually, a rat does not take water during a meal, but has a long drink after eating. At least 70 percent of water drunk is taken after meals in this way. But sometimes a rat takes small amounts of water while eating—behavior called prandial drinking by Teitelbaum & Epstein [666]. Prandial drinking is displayed by animals whose salivary ducts have been ligatured; it occurs when dry food is being eaten, and is evidently induced by conditions in the mouth. It can be prevented by injecting very small amounts of water into the mouth during a meal; injecting similar amounts into the stomach does not have this effect.

The importance of signals from the alimentary tract is also illustrated by the work of Deutsch & Jones and of Wiener & Deutsch. Rats given a choice between water and hypotonic saline drink more of the saline. This has been supposed to reflect a preference for the taste. Yet rats offered hypotonic saline and water as alternative rewards in a **T**-maze learn to go to the *water*. The explanation proposed by these investigators is based on the high rate of spontaneous firing of the sensory nerve fibers which are influenced by water or saline in the mouth; water reduces the rate of firing, while saline has a smaller effect: from this point of view saline is diluted water. Deutsch and his associates suggest that a rat continues to drink until a certain amount of water has been signaled, and that more saline has to be drunk than water to achieve this [199, 713].

4.4.3 Food

4.4.3.1 *The daily rhythm.* The knowledge we have of the control of eating suggests conclusions similar to those on drinking. As M. I. Grossman shows, the internal processes involved are multiple [274]. Again there are the divisions of food seeking, ingestion, cessation of eating and absorption.

Rats with access to shelter and to food eat at fairly regular intervals. White rats with access to food at a short distance from their nest have a cycle of three to four hours, and feeding coincides with the later part of a period of maximum general activity. Le Magnen & Tallon have described such cycles, but observed a good deal of individual variation in the feeding rhythms of albino rats. This is a common feature of the performance of animals in experiments on behavior. It is a source of difficulty for experimenters, which is perhaps why its existence is often ignored or glossed over. Nevertheless, some rats display a fairly consistent circadian (twenty-four-hour) rhythm: the modal interval between meals is about 140 minutes, and the amount eaten at each meal, 2 to 3 g. Meals taken during the night are larger than those eaten in daytime: hence nocturnal consumption is about 50 percent higher than that during daylight [405].

The greater consumption of food during darkness had already been observed in other researches, reviewed by Bolles [100]. Circadian rhythms are usually recorded in laboratories in which there are unchanging periods of dark and light, each of twelve hours. Conditions are similar near the equator, but not elsewhere; and in no major natural environment are the nights always wholly dark.

H. V. Thompson [672], in work already cited, has described the feeding rhythm of wild rats. In the natural environment (a pig farm) in which he made his observations, the rats fed almost wholly at night. This was probably not a consequence of some autonomous rhythm, but was imposed by the cycle of light and darkness and by the absence of disturbance by man at night. By making food available at a particular time, Thompson trained rats to feed at that time. The feeding rhythm, and activity rhythm in general, displayed by rats, is evidently a product of an interaction between internal and external factors.

4.4.3.2 *Stimuli from the gut.* Among the internal factors, as with drinking, are stimuli from the gut. The activity cycle of rats is paralleled by one in the muscles of the stomach. Powelson used an operation in which the stomach of a rat is shifted to a position between the skin and the abdominal wall; here its movements can be both seen and automatically recorded. Gastric peristalsis reached a peak at the time of greatest locomotor activity; sometimes the peristalsis began before the general movement, but more often the rat started to move around before peristalsis began [526]. Overt activity, at least of adults, therefore does not depend on gastric movements; moreover, the activity cycle persists even if the stomach has been surgically removed, or the nerves to the stomach have been cut. Feeding, too, persists after these operations. There is, however, still the possibility that impulses from the stomach and intestines play some part in inducing feeding behavior: the findings show only that the stomach does not play a *necessary* part.

There is, indeed, good evidence that impulses from the gut influence eating, but its end rather than its beginning. M. Smith & Duffy have examined the effects of bulk of the stomach contents. Rats were allowed to feed for only two hours in each twenty-four, during which the effects of various previous treatments were studied. Some received a mixture of kaolin and water, others, kaolin and glucose solution isotonic with body fluids. The mixtures depressed eating to a similar extent. The rats were evidently responding to increased volume of the stomach contents by ceasing to eat [624].

The influence of stimuli from the alimentary tract can also be illustrated by comparing the effects of taking food through the mouth with those of having it injected into the stomach through a fistula. Kohn measured "hunger" by the readiness of rats to operate a panel which, when pushed, released a drop of liquid food. One group had 14 ml milk injected straight into the stomach; a second had 14 ml saline injected in the same way; and a third were allowed to drink 14 ml milk in the ordinary manner. "Hunger" was found to be lower after stomach milk than stomach saline, and lower still after mouth milk. Since the test for hunger was applied 5.5 minutes after ingestion of the milk, the effect was rapid (figure 32). Mook has confirmed the contribution made by stimulation of the upper part of the alimentary tract, and has also brought evidence of osmotic effects on intake, acting in the stomach [477].

Nevertheless, intake can be regulated when there is no input from the mouth, pharynx or esophagus. Epstein & Teitelbaum maintained rats with a permanently implanted stomach tube; the rats were able to move freely. They were not allowed to eat but, if they pressed a bar, food was injected into the stomach. (The rats had already been accustomed to bar-pressing.) They soon learned to press the bar at a rate which gave them the energy intake to maintain their normal weight [223].

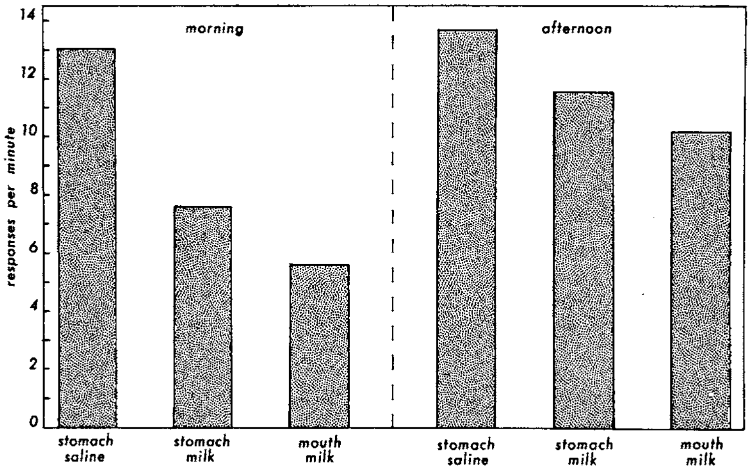


Figure 32. "Hunger" and its satisfaction. Rats in a cage could obtain food by pushing a panel. The different satiating effects of saline injected directly into the stomach, milk injected into the stomach and milk taken by the mouth are compared on two occasions in one day. (After Kohn [376].)

4.4.3.3 *Internal States.* None of these experiments helps us to understand the *onset* of feeding. A common sense hypothesis is that an animal eats when it needs food. This notion has two aspects. First, it might imply the more colloquial statement that an animal eats when it is hungry. A man knows he is hungry by his feelings; but we know nothing, and can surmise only a little, about the feelings of rats: if we wish to speak of a rat's being hungry we are obliged to base such a statement on observation of a rat's behavior or internal state. The relevant behavior consists of moving about, and of eating when food is reached. In an experimental situation, such as a Skinner box (plate 24), the behavior could include pressing a bar or other learned act. Hence in ethological statements the word "hunger" could be defined either as the tendency to eat or, if preferred, as the internal state which tends to induce eating; in any case, the events referred to in the definition should be of a kind that can be observed by anybody. Whatever the exact definition, talk of hunger provides no explanation of a rat's behavior: it does not help one to predict what a rat will eat or when, but merely *names* a type of behavior or internal state.

The second aspect of the notion, that a rat eats when it needs food, is heuristically more useful. It entails asking certain questions. What is meant by "needing food"; or what is the criterion of "need"? If the concentration of glucose in the blood falls below a certain level, the animal becomes comatose. Blood sugar level is fairly rapidly affected by eating, and so might determine the onset of feeding. This is the basis of the glucostatic hypothesis of Mayer. It has been tested in various researches, of which an example is that of M. Smith & Duffy already cited. They introduced a glucose solution, isotonic with body fluids, into the stomach by a gastric fistula; in this way effects of taste and swallowing were excluded. No depression of eating followed [624]. Another means of getting glucose straight into the body, used by Janowitz & Grossman, is to inject solutions intraperitoneally. This led to a slight depression of food intake, but not more than followed control injections of saline of the same volume. These investigators went on administering glucose in amounts equivalent to 25 percent of the energy needs of the rats for up to seven days, and still the animals failed to adjust their feeding to the excess [343]. The blood sugar hypothesis, then, is contradicted by the experimental evidence, at least for rats.

A second suggestion, made by Brobeck, has been briefly expressed as follows: "Animals eat to keep warm, and stop eating to prevent hyperthermia" [110]. The food intake of rats declines with rising environmental temperature, until above 34°C they develop a slight fever and almost completely stop eating, though their metabolic rate is raised at this temperature. Brobeck suggests that they could not, in these conditions, stand the additional heat stress that would result from the specific dynamic action (SDA) of ingested food. As a test of the hypothesis, the satiety value of different diets was related to their SDA. The hypothesis requires, for instance, that a diet containing much protein (with its high SDA) would be accepted in smaller amounts than a high fat diet. The findings agreed with the hypothesis [112].

One question is what significance should be assigned to the evidence, given above, for the influence of stimuli from the alimentary tract on feeding. Perhaps the effects of bulk in the stomach, and of tasting and swallowing, are the results of early experience. These effects can bring about a decline in eating before any foodstuffs actually enter the blood; but in the life history of an animal the gut stimuli must have been regularly followed by the primary actions of foodstuffs within the body. Such actions include the effect on body temperature. A rise in temperature may come to be associated with the prior experience of food in the mouth and in the stomach; and so the stimuli from the gut come to evoke the response which previously followed a rise in temperature, namely, cessation of eating.

Brobeck's proposal allows a discussion on the sort of physiological analysis that might account for the fact that an animal starts to eat and later stops, but there is no convincing evidence that a change in body temperature is the crucial factor in normal circumstances [631]. S. P. Grossman & Rechtschaffen have studied variation in brain temperature in relation to food intake. They confirm that eating leads to a rise in the temperature of various parts of the brain; but this is not a necessary or sufficient condition for the animal to stop eating. (i) The animal continues to eat after the maximum temperature has been reached; (ii) the normal temperature is rapidly restored, regardless of the size or duration of the meal; (iii) eating is unaffected by variation in brain temperature such as occurs, for example, after activity [275].

A third proposal, made by Kennedy, is that the relevant internal state is the fat balance, or the size of the fat stores. Young rats maintain their adipose tissue organs in a remarkably constant state, apparently as a result of sensitivity to the concentration of metabolites (as yet unidentified) in the blood. Kennedy's hypothesis is, then, a "lipostatic" one [361–2].

A possibly related finding is the relationship between body weight and feeding behavior. Until recently, in experiments on the effects of a food deficit, the duration of fast has usually been varied; the expected result was then a proportionate change in behavior, for example, in the amount eaten at each meal or in the readiness to start eating or to work for food. But the effects of fasting (reviewed by Bolles [100]) are not always consistent. An alternative procedure, originally due to Stolurow [653], is to supply each animal with rather less food than would normally be eaten. In this way, body weight can be reduced to, and held at, a fraction (say, 85 percent) of what it would be if food were given in excess. Since, as we know, eating usually maintains a steady body weight or growth rate, this method might be expected to have a consistent effect, from one animal to another, on behavior. And so it often has: for instance, the readiness with which rats will accept food flavored with an aversive substance (quinine) increases systematically with percentage loss of body weight [100].

4.4.3.4 *"Hunger" and its definition.* The word "hunger" now requires discussion. Hebb has made an important statement on this subject, though in a logically defective way. He begins by defining hunger as the tendency to eat—a definition, however brief, in terms of behavior. Later he asks his readers to "consider hunger to be . . . an organized neural activity" [307]. This is an example of the tendency to allow a term to slide unobtrusively from one meaning to another which has bedeviled so much writing about behavior. Hebb here wishes to direct attention to the neural activities which underlie feeding; an organized neural activity can be aroused, or quelled, in more than one way as a result of habit formation: owing to association, stimuli from a variety of sources can come to activate a pattern of central nervous activity which leads to, or inhibits, feeding.

Another example of difficulty with the meaning of the term "hunger" may be found in a valuable review by N. E. Miller of the relation of food consumption to other aspects of feeding. His formulation is that food consumption is not a satisfactory measure of hunger, but he does not define hunger. In one situation, fasted rats are trained to press a bar which delivers a food pellet into a dish below. When a rat has been trained, the mechanism is set to deliver a pellet only irregularly and unpredictably. Miller writes: "The animals continue working much like a gambler who operates a slot machine in the hope of hitting the jackpot. The rate at which they work seems to be a good measure of the strength of hunger." The implication of the last sentence is that there is some process or state (named "hunger"), which *could* be directly observed, but is conveniently measured indirectly by the rate of bar-pressing.

Miller describes a second situation in which rats are presented with small samples of food, each containing a slightly higher concentration of quinine than the last. The hungrier the animal (that is, the longer it has fasted), the greater the concentration of quinine it will accept. Miller then refers to the behavior of rats which have hypothalamic lesions and consequently eat more food than normal rats (§ 4.4.5.1). They become obese, but press a bar for food *less* vigorously than normal rats; and they are *more* easily deterred by the taste of quinine [461].

Clearly, bar-pressing and the quinine technique do not measure the same internal processes as food consumption. An important distinction, as Bolles [100] shows, is between the *initiation* of feeding and the amount consumed once feeding has begun. Bar-pressing and quinine are "pre-ingestion measures" of internal state. Rate of bar-pressing increases with the length of fast. Similarly, the interval between giving the opportunity to eat and the actual start of feeding (the *latency*) declines with the level of deprivation. In contrast, the amount consumed is influenced by what happens after food has begun to be eaten. Whether one says that one or another experimental procedure measures "hunger" should depend on what meaning has first been given that term.

In further experiments by N. E. Miller, rats had two fistulae, one into the stomach, the other into a balloon in the stomach. When milk was injected into the stomach, bar-pressing to get food was reduced; when fluid of equal volume and specific gravity was injected into the balloon (thus increasing the volume of the stomach contents but not the food supply) bar-pressing was again reduced, though not quite so much. Hence both had a satiating effect. Similar rats were trained in a T-maze: one group was rewarded, on turning to a given side, by injection of milk into the stomach; the other received an injection of fluid into the stomach balloon. The first group duly learned to turn to the side where the milk was given; but the second learned to *avoid* the side on which the balloon was inflated: inflation of the balloon was punishing, not rewarding. Miller suggests that the reduction of bar-pressing which followed inflation of the balloon was not an effect of satiation but rather a consequence of nausea [461].

The general conclusion is not that food consumption is an inadequate measure of hunger, since that begs the question of what the term "hunger" means, but that there are many internal processes which influence feeding. There is no single process or state which can conveniently be named "hunger" or "hunger drive"; the internal springs of feeding behavior are diverse, some acting together, others in opposition. Table 1, adapted from Brobeck [111], provides a brief scheme.

4.4.4 Sodium Chloride

The concept of hunger includes the notion of special hungers, for instance, for salt. Fregly [244] and Pfaffman [524] have discussed the regulation of intake of sodium chloride. A normal laboratory rat, given a choice between hypertonic salt solutions on the one hand, and hypotonic or isotonic solutions on the other, takes mainly the latter. If a rat is deprived of salt, or has both its adrenal glands removed, there is a compensatory increase in the amount of salt ingested.

TABLE 1. FACTORS IN FOOD INTAKE

Initiate or increase feeding	*"Reflexes"*	*Stop or decrease feeding*
Lowered supply of glucose	Sense organs (olfactory, gustatory, etc.)	Exercise
Decline in body temperature	Sensory neurons	Dehydration
Cold environment	Brain stem "centers"	Rise in body temperature
Contractions of empty stomach	Motor neurons	Warm environment
	Muscles	Stimuli from mouth and pharynx
		Distension of stomach

Two kinds of process could be involved in regulating salt intake. First, preference might be shown for salt, or for salt in solution, only when the taste or some other cue had been followed by a particular change in the state of the body. This would be an instance of habit formation, or learning from experience, and requires that the substance should have a fairly rapid (and presumably beneficial) effect. Second, a deficiency of salt could lead to an immediate change in behavior, perhaps dependent on a change in the response to the specific taste of sodium chloride. Salt would then be attractive without regard to its after-effects. This would be expected only when (i) the substance had a distinctive taste, and (ii) it was present in food or drink in amounts sufficient for the taste to be effective. The second requirement might not apply, say, to vitamin B_1 (thiamin).

Epstein & Stellar used adrenalectomized rats. Some of the rats were allowed access to salt only after a severe state of deprivation had been reached. These rats began drinking large amounts of salt solution at once; post-operative experience was not necessary.

An important question is whether such behavior is related to a change, perhaps resulting from a lowered blood salt level, in the response of the taste organs to salt. Epstein & Stellar used an ingenious method to investigate the influence of taste in stopping drinking. They administered ion exchange resins in such a way that rats drank, and tasted, a 3 percent NaCl solution, but actually absorbed through the gut wall only as much salt as would have come from a 1.5 percent solution; the rest of the salt was taken up by the resins. The rats then drank as much salt as they would have taken had the solution itself contained only 1.5 percent NaCl: that is, they drank the amount appropriate to bodily need; the effect of the internal environment was greater than that of taste [222].

Nevertheless, in some situations habit formation dependent on taste is important. Adrenalectomized rats were allowed access to 3 percent NaCl immediately after the operation, and not after a delay while deficiency developed; they then only gradually overcame their usual aversion from the salt solution, but eventually acquired the physiologically necessary habit of drinking it in large amounts. In this gradual change of behavior, it may be suspected, the taste of the salt acted as a "cue" or stimulus which came to be associated with its internal effects; the salt thus constituted a reward [222].

These findings conform with observations by Pfaffman. He recorded the electrical activity of the sensory nerve fibers from the tongue, in response to sodium chloride and other substances; there was no change when internal bodily states altered behavior toward the substances [524]. Correspondingly, Falk & Herman found a rapid change in behavior due to salt depletion, which they attributed to central, not peripheral, changes. Their rats normally preferred distilled water to 3 percent salt solution. The rats had their body Na^+ depleted, not by an inadequate diet, but by intraperitoneal dialysis. The result was a rapid change of preference in favor of the salt solution [232].

In all such experiments, the emphasis is on changes in the central nervous system related to need for salt; but, as we must expect from our knowledge of the regulation of energy intake, the external senses play a part. To illustrate this, there are first some anomalous observations by Fregly and his colleagues. They fed rats with food mixtures containing varying amounts of sodium chloride, up to 6 percent by weight. At the same time, solutions of sodium chloride were offered as an alternative to plain water. It might be expected that, when the proportion of salt in the food was high, the readiness to drink salt solutions would decline; but this was not found. The balance between salt and water in the body was instead maintained by an increased consumption of water. These authors suggest that sodium chloride intake is regulated in part from the input from the mouth and pharynx, determined by the proportion of sodium chloride dissolved in the saliva [245]. Experiments by Nachman & Valentino conform with this hypothesis. They injected sodium chloride solution directly into the stomach of some of their rats, and found no effect on the readiness with which the rats took sodium chloride solutions. Similar amounts of salt taken by drinking did lead to satiation, that is, to refusal of more salt [494]. M. H. Smith and others have ingeniously controlled for the effects of what is ingested. They gave their rats a choice between saline and glucose solution, but arranged that when the rats drank saline, they received glucose intragastrically; and when they drank glucose solution, they received intragastric saline. In these conditions, sodium-deficient rats still took more saline than glucose [625]. Observations of this kind suggest that the input from the periphery may determine at least when an animal *stops* taking salt.

The work on salt ingestion illustrates further how feeding may, in varying circumstances, be influenced by a diversity of incentives. The regulation of total food intake, of the intake of sodium chloride and of the ingestion of other dietary components—each of these has its internal mechanisms, partly independent but sometimes, as with food and water, obviously interacting [657].

4.4.5 The Central Nervous System

4.4.5.1 *Over-eating.* Granted that eating and drinking are regulated by internal states, such as the composition of the blood or the tonicity of body fluids, there remains the question of the apparatus which responds to the peripheral changes. It is possible to make a sated animal eat or drink by injecting into the brain, with a micro-pipette, minute quantities of drugs. There are several regions of the limbic and diencephalic systems which respond in this way. Coury, who has described such experiments, suggests that there are separate but structurally dovetailed systems ("synaptic nets") which regulate eating and drinking in all parts of the brain, including the neocortex [176]. Unfortunately, as yet, there is little experimental evidence except on the hypothalamus, and especially on the disturbances of feeding brought about by damaging that small structure in specific ways. Bruce and Kennedy injured the tuberal area of the hypothalamus on both sides and so produced exceedingly obese rats; the increase in body weight was due to excessive eating. (Figure 33 illustrates this from another study.) There was a constant relationship between the energy value of the diet and the increase in body weight, regardless of the composition of the diet: that is, high fat or high protein diets failed to alter the effects of the lesions. In the same way, control animals kept a constant weight despite changes in the composition of the food offered. Food intake (as we have seen) is "calorimetric"; and these experiments show that the *cessation* of eating depends on the functioning of specific groups of hypothalamic neurons [118]. Although the lesions are not repaired, the voracious behavior is only temporary: after some weeks each rat, having attained a remarkable fatness, resumes a nearly normal intake without reverting to a normal body weight [360].

May & Beaton have given a further description of the two phases of hyperphagia: the early dynamic, and the late static. They made electrolytic lesions in the ventro-medial nuclei of the hypothalamus on each side. In the first phase there was a great increase in food consumption, a corresponding gain in body weight, lowered activity, and a change in the circadian rhythm of eating, so that food consumption was evenly spread throughout the twenty-four hours. In the second phase more food was still eaten, but only enough to keep the increased weight fairly steady. Resting oxygen consumption was about that of the controls in both phases. The experimental rats laid down great masses of fat in their adipose tissues; and these tissues, studied in vitro, laid down fat at a higher rate than those from control rats [443]. These observations give us a glimpse of the many changes, down to the sub-cellular level, which must accompany an alteration in behavior such as hyperphagia.

Hypothalamic hyperphagia evidently involves a change in the setting of some system which regulates body weight: it is not a case of complete destruction of a control system. Hoebel & Teitelbaum have illustrated this further by using another method of inducing obesity. They administered insulin twice daily for two weeks. Some of their subjects failed to survive this drastic treatment, but those that did, doubled their food intake and gained weight correspondingly. When the treatment was stopped, the rats took little or no food until their weight was back to normal. In further experiments, rats were kept on insulin for four months, and so gained about 210 g. The ventro-medial hypothalamic satiety center was then destroyed on both sides. As we have seen, this normally induces hyperphagia; but the rats which were already obese displayed little over-eating or further gain in weight. Similarly, force-feeding hypothalamic obese rats can make them even fatter than they would ordinarily become; when the force-feeding is stopped, they eat less than usual until they restore their normal obesity [328].

The injuries made in the brain in these experiments destroy only a few hundred cells on each side: the technique is impressive, and the results encourage the belief that real progress is being made in unraveling brain function and in revealing the physiology of feeding, even though any method which depends on destruction is crude and unsatisfying. We have seen that eating can, however, be provoked also by local application of drugs; and some experimenters have made rats over-eat by electrical stimulation. Stimulation is not of the ventro-medial region, or satiety center, but of the lateral hypothalamus. Steinbaum & Miller stimulated the lateral hypothalamus of rats for two hours a day for thirty-one days, and induced excessive eating and consequent obesity. The food offered was a wet mash. In other experiments a mixture containing a high proportion of fat was used. The result was a still higher rate of energy intake during the period of enforced feeding; but this was balanced by a lower intake during the remaining twenty-two hours in the day [645].

Hence, the abnormal behavior evoked by electrical stimulation has properties similar to those of behavior resulting from lesions visible under the microscope. Electrical stimulation of the lateral hypothalamus (ESLH) can also provide the internal state which evokes habit formation with food as a reward. In ordinary experiments with food as an incentive, the animals to be trained are first fasted (§ 8.3.1). But Mendelson & Chorover were able to use continuous ESLH instead: their rats were satiated, but still acquired a discrimination in a **T**-maze for food [454]. Similarly, Coons and others trained rats to press a bar in a Skinner box (plate 24) under ESLH [169].

Accordingly, Coons and his colleagues equate ESLH with "hunger"; but, as Ball has shown, this is a dubious equation. He too studied the behavior of rats which were provoked to feed by ESLH. The feeding response increased with increasing duration of the ESLH, up to 6.3 sec. He also gave his rats the opportunity for self-stimulation, in conditions which allowed them to vary the duration of the ESLH; the preferred duration was then found to be two to three seconds. He therefore rejects the assumption that the rewarding effect of self-stimulation is neurally equivalent to the rewarding effect of a consummatory response such as feeding [32].

Earlier in this chapter we saw something of how normal eating is influenced by the taste of foods. The sensory input from the mouth and pharynx also plays a part in the behavior of hyperphagic animals. McGinty and his colleagues made hypothalamic lesions of the kind which usually induce hyperphagia, but allowed their animals to feed only through a stomach tube; the amount consumed was under the control of the rats, but the food could not be tasted or smelled. The rats nevertheless ate more than the normal amount, but they did not achieve the level of obesity reached by rats feeding in the usual way. The authors therefore conclude that the oropharyngeal input influences both the rate and the duration of excessive eating [450]. In these experiments the rats had to work to get food, and they were displaying the well-known reluctance of hyperphagics to exert themselves. If rats in such conditions are given small amounts of food to taste, they work harder [667].

Panksepp has further illustrated the peculiarities of hypothalamic hyperphagia. His rats had the usual bilateral lesions of the ventro-medial hypothalamus, and were tested for their ability to adapt their feeding behavior to fasts of up to twenty-four hours, or to being allowed food for only one hour a day. The control rats, as expected, adapted by increasing their rate of feeding, but the injured rats did not; yet the latter, when allowed to do so, over-ate and became obese. Evidently injuring the ventro-medial hypothalamus upsets the animal's response to a deficiency of food as well as its adjustment to repletion [516]. But this is far from the whole story, even if we confine ourselves to the hypothalamus, as we now see.

4.4.5.2 *Anorexia.* Anand & Brobeck made minute injuries in different regions of the hypothalamus. Damage to the ventro-medial nuclei produced the overeating and obesity already described. At the same level, in the extreme lateral part of the lateral hypothalamus, they found a region of which destruction on both sides led to a complete failure to eat. This is in the region, mentioned in the previous section, of which electrical stimulation induces hyperphagia. Evidently, the very small groups of cells concerned have quite specific functions, since damage on a similar scale in regions near the nuclei mentioned does not have the same effect. If both the ventro-medial and the lateral nuclei are destroyed, the result is the same as destruction of the lateral centers alone: the animal stops eating [15]. This suggests that the ventro-medial group acts by inhibiting the lateral "feeding" centers; and Oomura and others have indeed found a reciprocally inhibitory effect between the two regions [512].

Many experiments of this sort illustrate further the difficulty of devising methods to cope with the fine detail of neural function. S. D. Morrison & Mayer made minute lesions in the median eminence of the hypothalamus of rats: adipsia was the main effect, but aphagia also developed. Further, the regions in which lesions produced the greatest effect on drinking also had a maximum influence on eating [483–4]. Other experiments illustrate once again the importance of exteroception. We know that brain lesions which lead to behavioral or sensory defects are often followed by gradual recovery of function. This is shown by rats in which hypothalamic damage has completely inhibited eating. When Teitelbaum & Stellar kept such aphagic rats alive, initially by feeding them through a stomach tube, feeding behavior was restored in from six to sixty-five days. The rats regained and then held their original body weights. Before complete recovery, the animals had to be tempted to eat by being given wet, highly palatable foods; among these were biscuits and chocolate. After recovery, the rats' feeding behavior was changed: unlike control rats, they ate much corn oil when this was offered; the recovered rats were also slower than controls to adjust their energy intake to an increase in the non-nutritive bulk in their diet [668].

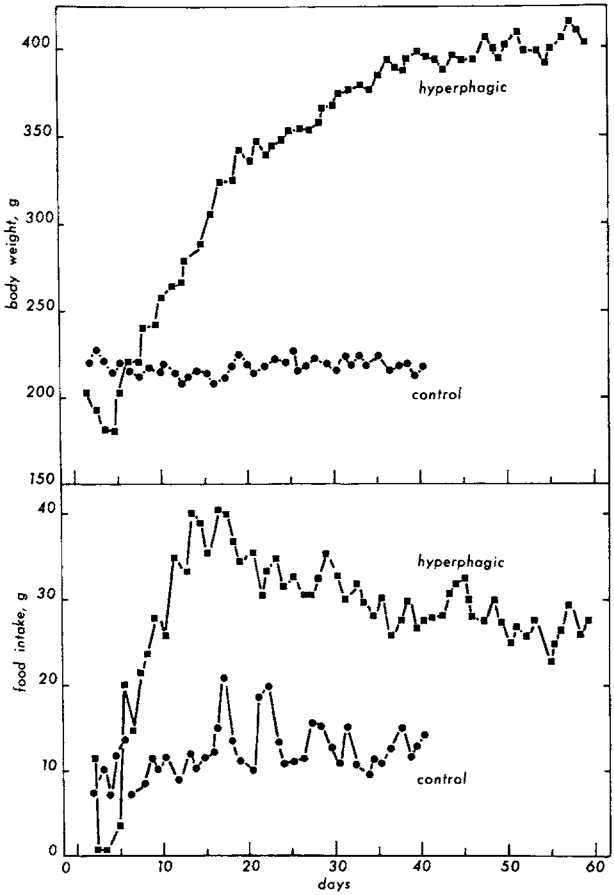


Figure 33. Effect of lesions in the ventro-medial regions of the hypothalamus: initial over-eating and a doubling of body weight. The operation was on the second day. (After Teitelbaum [664].)

In other experiments, rats recovered from lateral hypothalamic injuries have kept their body weight at a consistently lower level than that of controls. Accordingly, Powley & Keesey underfed rats *before* operating on them; hence at operation they were already under-weight. The post-operative period of aphagia or anorexia was then brief or absent. In their view, the "lateral hypothalamic feeding syndrome" is, like the ventro-medial, due to a resetting of a system that regulates body weight [527].

In nearly all experiments of this kind, the lesions are bilateral. Gold, however, has made small lesions of the lateral hypothalamus on one side only. Some led to an aphagia which lasted up to four days, or adipsia which lasted rather longer. The rats were allowed to recover. Lesions were then made on the other side, and produced the effects typical of the usual bilateral operation [263]. This finding is in contrast to that of Stein and others [644] described in § 2.2.2.

The remarkable findings from studies of the hypothalamus could lead to a distorted picture of brain function. A corrective is provided by Parker & Feldman, who made large, bilateral lesions in—for a change—the reticular formation (§ 2.5) of the midbrain. The result was both aphagia and adipsia. Smaller injuries in the same region led to alterations of feeding behavior similar to those that follow damage to the lateral hypothalamus [518]. These findings give some hint of the interactions which must, in the normal brain, take part in the regulation of ingestion. Further critical comment has been made in a review by Valenstein and others, who question the interpretation of hypothalamic function in terms of distinct "centers" [689].

The study of aphagic or hypophagic animals has led to an instructive controversy. Rodgers and his colleagues have tried to formulate questions on the precise nature of the deficit in hypothalamic hypophagia. Is the failure to eat "motor"? That is, is it due to "damage to the neuronal systems that organize the movements of feeding"? Or is it "motivational"? In the second case, according to these authors, "the animal is able to eat, but it does not because it is not hungry" [553]. The phrases quoted are a curious mixture of references to physiological processes, which could in principle be identified, and expressions which seem to refer to the feelings of the animals studied. They are, however, supported by reference to actual experiments. The "motivational" hypothesis is supported by the effects, already mentioned, of palatability: damaged animals can be persuaded to ingest fluids by means of well-chosen flavors. Rodgers and his colleagues also induced feeding movements by chemical or electrical stimulation of the hypothalamus; these observations are held to contravert the hypothesis of a motor deficit.

The opposite opinion has been stated by Baillie & Morrison: their rats (they say) "desired food but were unable to consume it." In their experiments, rats which refused to take food normally, as a result of hypothalamic damage, were induced to press a lever and so inject, directly into the stomach, fluid food; in this way the rats were able to maintain themselves. Accordingly, Baillie & Morrison suggest that the deficit was in the organization of the specific motor patterns of eating and drinking [31]. Morrison later reported observations on aphagic rats. Immediately after the operation they become almost continuously active. As they gradually recover their responsiveness to food, a more normal rhythm of activity and inactivity appears; in addition, self-grooming, which has ceased, is resumed. S. D. Morrison suggests that these observations are consistent with the hypothesis of motor disorganization as a cause of aphagia; but he also accepts that there are probably additional causes of total refusal to eat [481].

The papers cited in the two preceding paragraphs can be recommended as reading for research workers beginning experiments in this or related fields. The workers on both sides of the controversy achieve a high standard both of technique and of presentation. They also illustrate, no doubt inadvertently, the disadvantages of using terms such as "hunger" and "desire": when we attempt an analysis of the internal processes that underlie behavior, everyday expressions fail to match our observations; they even interfere with the drawing of appropriate conclusions. The need for a more rigorous language will become increasingly evident as our knowledge of central nervous function improves.

4.5 CONCLUSIONS

The distinctive feature of the diet of rats is its variety: instead of specializing in a particular kind of food, rats have specialized in omnivory. Accordingly they have a system of behavior which enables them not only to find food in a substantial area around their nest but also, to some extent, to select food according to need.

The exploratory behavior of rats keeps them informed on food supplies in their neighborhood; superimposed on it is an additional tendency to be active when fasted or in some other deprivations. All possible food materials are sampled, though some substances with (to man) strong tastes or odors are rejected. There are also certain fixed preferences, for instance for sweet substances.

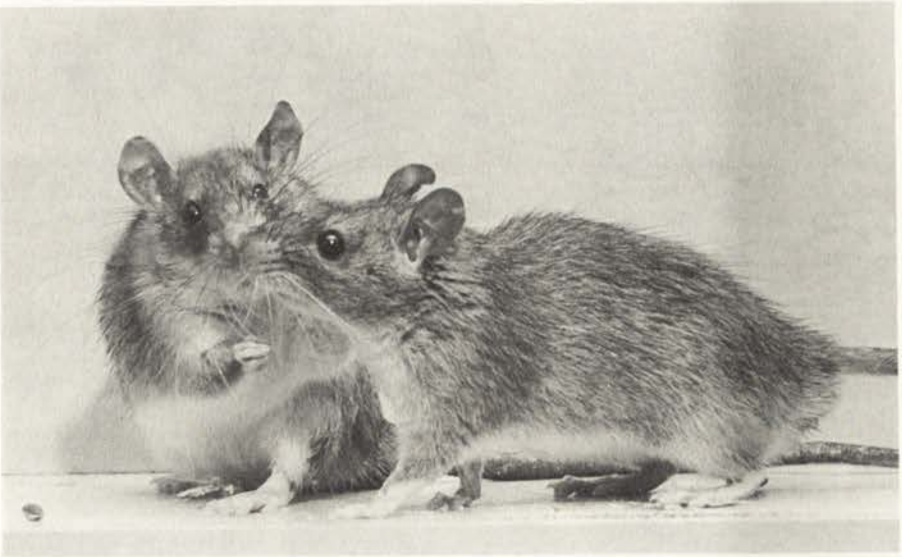
These preferences, seemingly independent of experience, have no evident homeostatic function; in detail they differ between wild and laboratory rats. The primary homeostatic effect of feeding is the maintenance of a steady energy intake. The selection of favorable foods, and avoidance of unfavorable (toxic) mixtures, both depend a good deal on habit formation: foods are sought or avoided according to their previously experienced internal effects, at least if these are fairly rapid.

Rats also have a number of activities related to feeding, for instance hoarding. These give further examples of the way in which a complex activity depends on an intricate interaction of fixed abilities with the effects of experience.

The study of the feeding behavior of rats provides an unusually detailed example of the physiological analysis of "drive" or "motivation" (chapter 10). Much is known of the internal processes which determine when eating and drinking begin, and also what makes them stop. The factors which control ingestion are both peripheral and central: peripheral effects include the responses of exteroceptors, the composition of blood and other body fluids, and also distension of the stomach; centrally, certain parts of the hypothalamus occupy key positions in the "control" of ingestion.

Much remains to be learned. Most of the methods used in investigating the central nervous system remain crude: even the smallest effective experimental injury indiscriminately destroys hundreds of neurons. As yet, we lack even a language in which a lucid account of brain physiology can be given: we speak of "centers" which "control" or "organize" or "co-ordinate" behavior, but such terms lack the precision we would like them to have. Moreover, it is not known what internal system provides the array of negative feedbacks which ensure that an animal maintains a steady, or a regularly increasing, body weight. There may be alternative systems which operate in different circumstances or at different ages. Blood glucose concentration and the magnitude of the depots of adipose tissue may be involved. The plurality of the internal processes which control feeding is reflected in the various indices of so-called hunger. For instance, the readiness with which a rat presses a lever for food is not correlated with its willingness to accept a distasteful mixture. No single concept, such as that of hunger, can profitably be used to refer to both the overt behavior and the internal processes described above.

Plate 1. Two wild *Rattus norvegicus* in a clash.



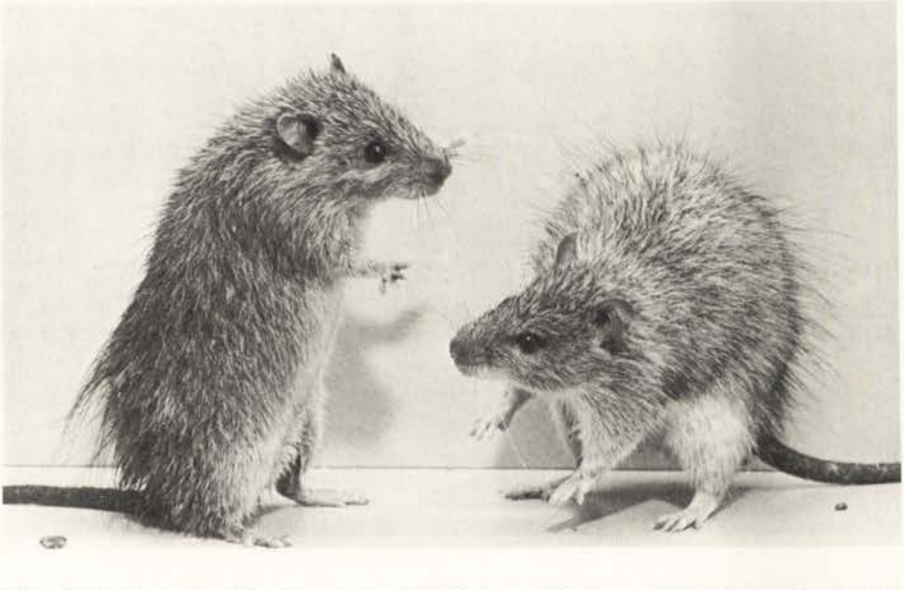


Plate 2. *Rattus rattus*, the house rat. Like *R. norvegicus* a world-wide commensal of man, but adapted to warmer climates.

Plate 3. *Rattus villosissimus*, the long-haired rat of central Australia. This species, normally independent of man, sometimes breaks out into massive plagues in grazing areas.

Plate 4. *Bandicota bengalensis,* the mole rat, of India, Pakistan, Burma and Malaya. This Murid, ecologically a counterpart of *R. norvegicus,* is present in vast numbers in both the crop fields and food stores throughout India and neighboring countries.

Plate 5. Taking food to cover. A large male wild rat (about 450 g) drags a lump of horse liver of about its own weight toward its nest. (From Barnett & Spencer [60].)

Plate 6. Dragging a fowl's egg (*Gallus*) from a hen's nest by the use of the forelimbs and head. (Netherlands Department of Agriculture.)

Plate 7. An experiment on food selection. A wild rat eats whole meal in preference to wheat grains or sugar. (From Barnett [36].)

Plate 8. Wild rats eating wheat during census baiting.

Plate 9. Recognition by odor. A male wild rat investigates another male. A similar posture is sometimes adopted when a female is approached (figure 49).

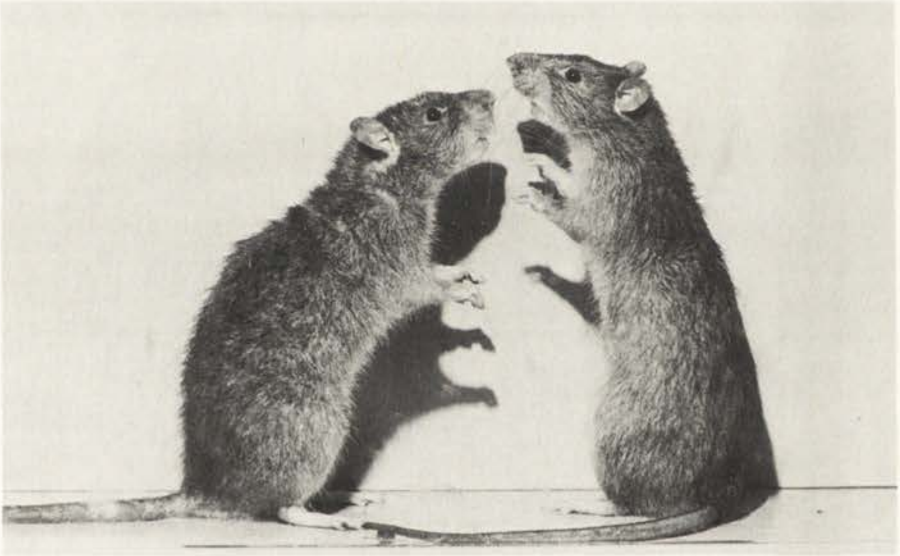
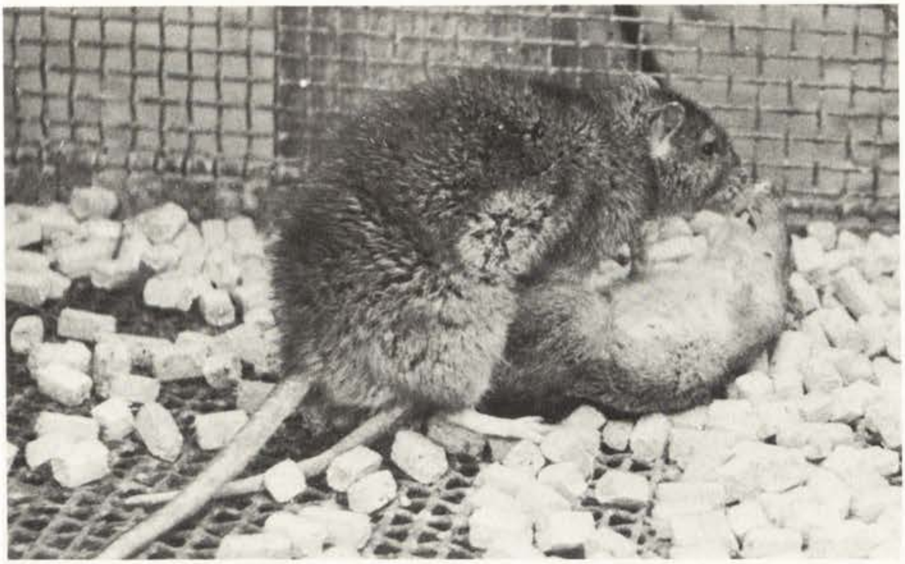


Plate 10. The threat posture of an adult wild male (on right) directed toward an intruder.

Plate 11. Boxing. Two wild male rats, one an intruder on the other's territory, face each other. The resident (left) has raised hair.



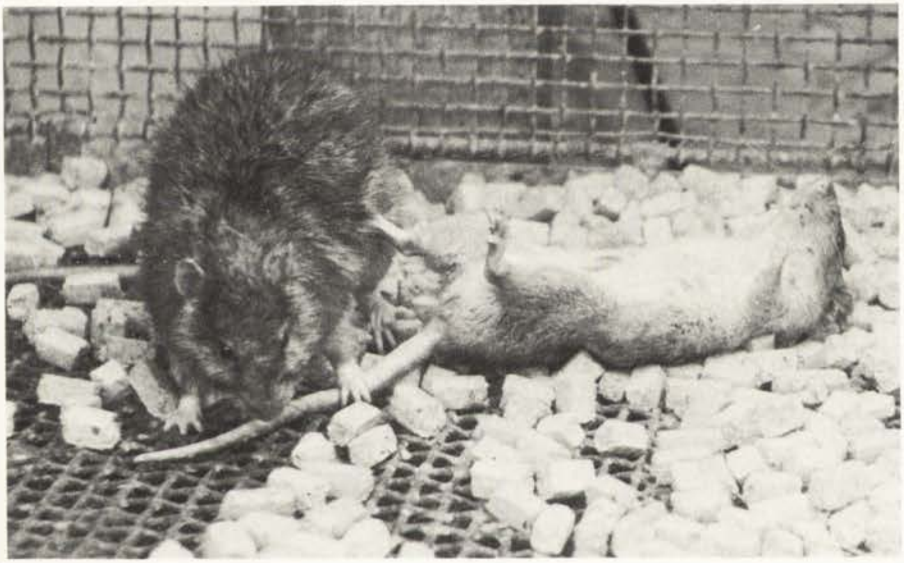


Plate 12. Attack. A male wild rat, though unwounded, collapses under attack.

Plate 13. The attacker of plate 12 sniffs the now motionless intruder; the latter no longer presents the constellation of stimuli which evoke attack.

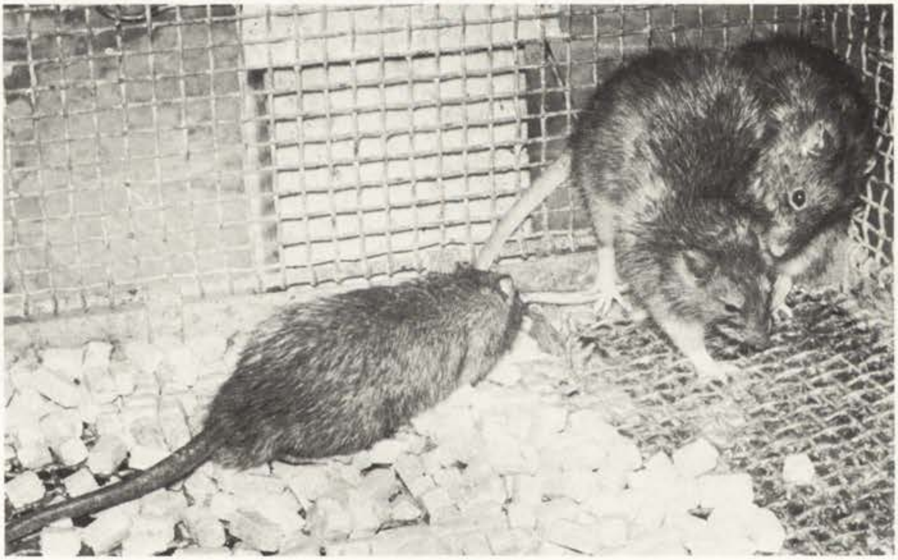


Plate 14. Attack. A resident male's leap lands him on an intruder (flattened ears), which fends him off.

Plate 15. Two adult males, of similar status, posture at each other. (Compare plate 10.)

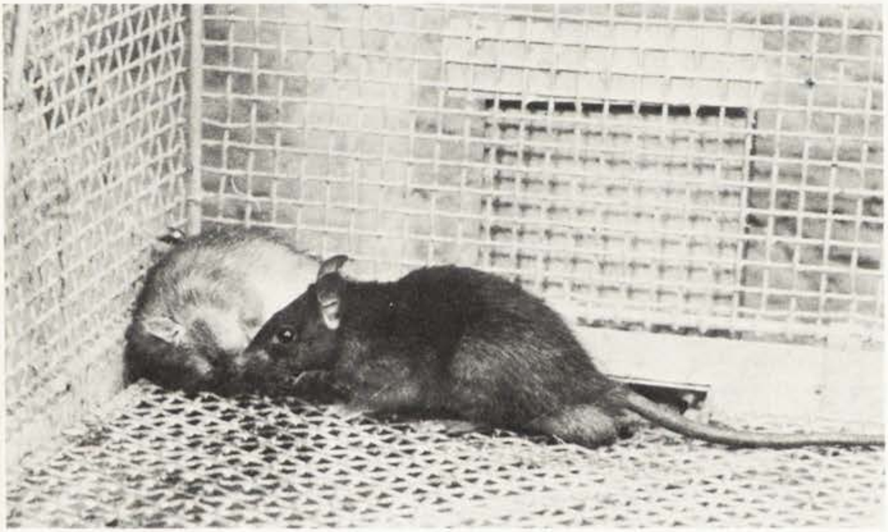
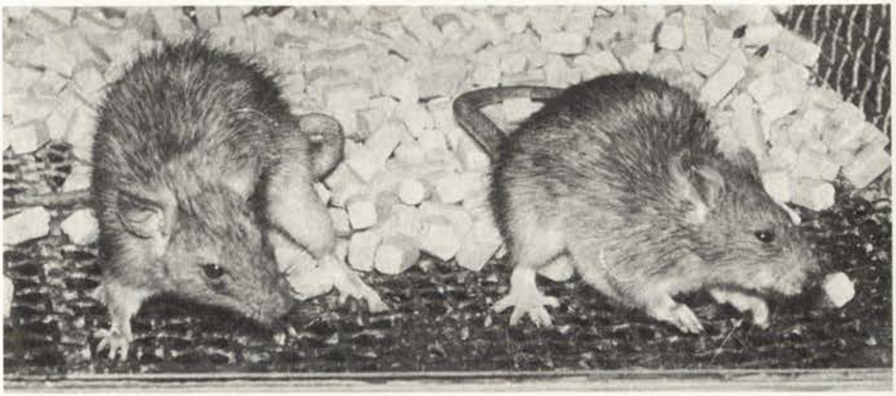


Plate 16. Interspecific interaction. Two *Rattus norvegicus* (left) and three *R. rattus* feeding together at a food tray used in experiments on feeding behavior. (From Barnett & Spencer [60].)

Plate 17. "Submissive" posture. In an experiment on interspecific relations, a male *Rattus norvegicus* newcomer adopts a non-attacking attitude on the approach of a resident male *R. rattus*. (From Barnett [37].)



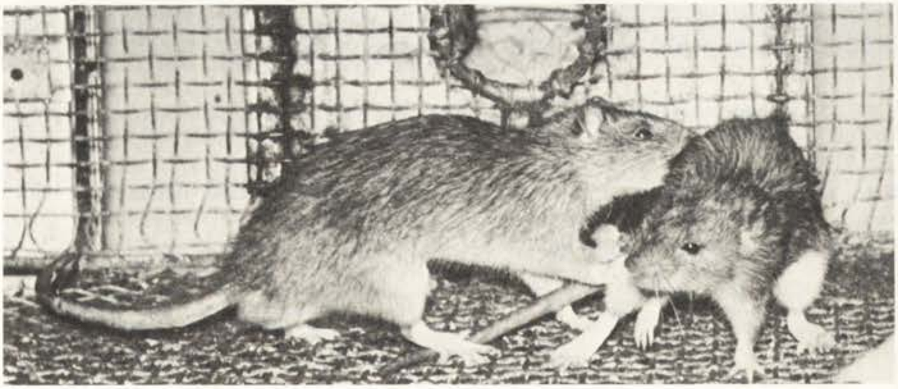
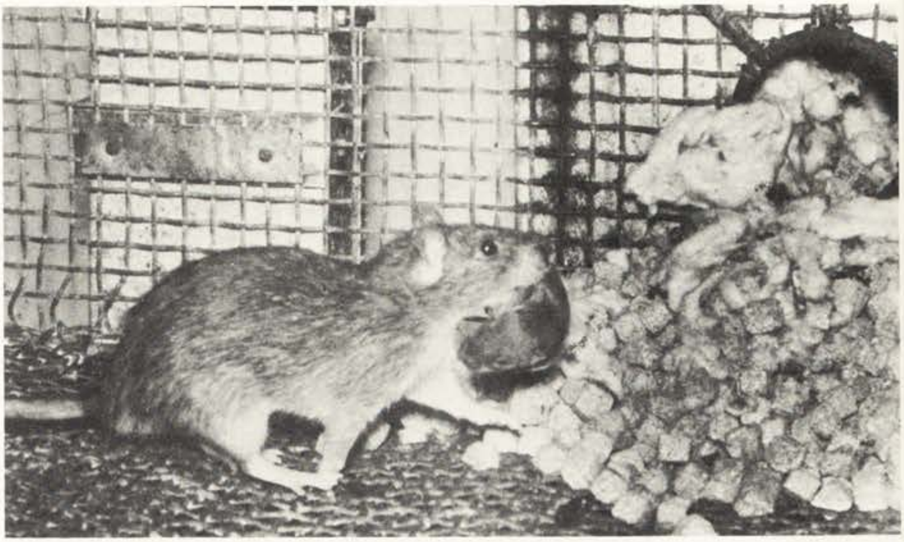


Plate 21. Female tending young aged 5 days.

Plate 18. Interspecific conflict. A momentary pause in a clash between a light-colored *Rattus rattus* (left) and a *R. norvegicus*. (1/1250 sec.) (From Barnett [37].)

Plate 19. A resident *R. norvegicus* makes a severe attack on a strange *R. rattus*. (1/1250 sec.) (From Barnett [37].)

Plate 20. Rejection of a male. A female not in estrus (right) kicks off a male trying to mount her. (1/1250 sec.)



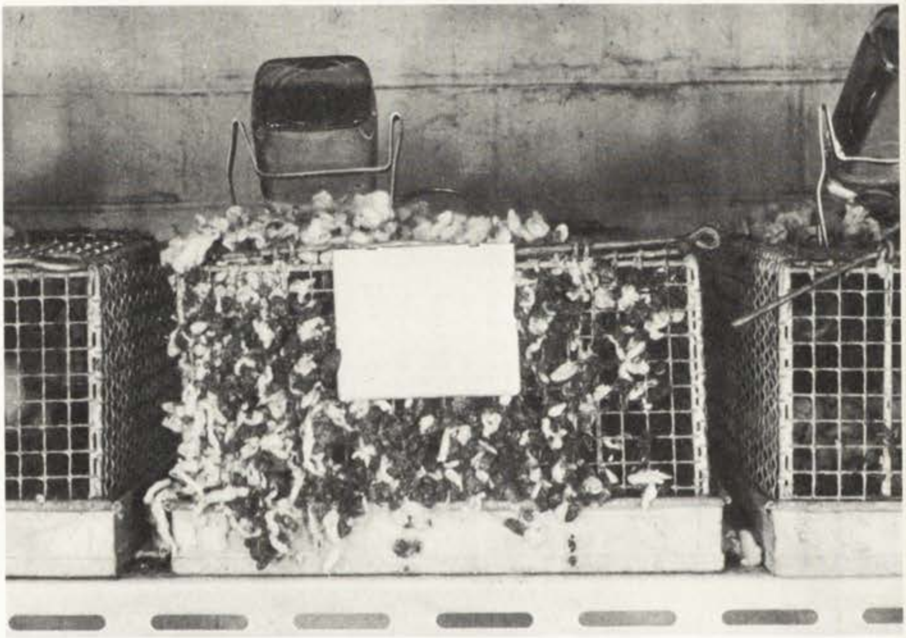


Plate 22. Female retrieves young.

Plate 23. Nest-building. A wild female with young has made a screen from a mixture of cotton wool, dung and peat moss stuck to the wire wall of a cage.

Plate 24. Skinner box, with laboratory rat. Pressing the lever may release a food pellet into the bowl. A light source in the background can be used as a cue (or a reward). The floor grid can be electrified to provide an aversive stimulus.

5 Social Interactions

There was speech in their dumbness, language in their very gesture.

Shakespeare

5.1 THE DEFINITION OF SOCIAL BEHAVIOR

In this chapter we turn to activities that ensure reproductive success rather than individual survival. Like all mammals, rats form family groups consisting of a female and her young; such groups are necessarily bound together during the period of dependence of the young on their mother. But rats, wild or tame, are also social animals in the sense that the adults too collect in groups. Wild rats live in colonies which have nesting sites and feeding grounds in common; there are evidently powerful influences which make them assemble together. At the same time there are disruptive elements in their behavior toward members of their own species: in certain circumstances wild rats even attack other rats.

This chapter, then, is on *social behavior*, that is, all behavior which influences, or is influenced by, other members of the same species. The term emphasized covers all sexual and reproductive activities, all behavior which tends to bring individuals together and also all intraspecific conflict. The preceding sentences constitute a *stipulative definition*. For reasons further discussed in the Appendix, the statements they contain cannot be "correct" or "incorrect": they express an intention to use the word "social" in a particular way *in this book*. The word is so used on the grounds of *convenience*.

Not all assemblies are social in the sense in which the term is used here. Members of one species often associate because they all respond in the same way to some feature of their environment, such as a source of food. Perhaps rats are sometimes brought together by the amenities offered by a particular area. To be suitable for rats, a biotope must offer food, cover and nesting sites and material. For *Rattus norvegicus*, cover may be (and away from buildings usually is) provided by earth burrows. We shall see, however, that there are severe restrictions on the extent to which strange rats can come together to form a stable group. Nevertheless, immature rats of both sexes, and adult females, could (as far as we know) form a colony in any area such as a large refuse dump, a glue factory, a food warehouse or a farm; throughout much of the world, all such places, in the absence of strenuous action by the human occupants, are liable to harbor large colonies of rats.

The social behavior of rats is often best studied in groups of wild individuals, either in conditions which approach the "natural" or in contrived situations which nevertheless permit the rats plenty of scope for varied behavior. Some early experiments on laboratory rats, reviewed by Munn, failed to demonstrate any tendency to assemble. Rats were put in an apparatus in which they had the opportunity to cross a barrier to reach another rat; in other experiments, rats were offered a choice between a compartment which contained both food and other rats, and one which contained only food. The only positive conclusion reached in these inquiries was that rats possess a strong "exploratory drive" [490]. The importance of choosing the right kinds of rats and the right conditions is shown in a further statement by Munn: "Relatively little research has been done on social behavior in rats primarily because rats are not especially influenced by each other's actions" [490]. The second part of this statement is mistaken. It arises from the concentration of psychological research on domestic varieties in conditions which leave little scope for social interactions.

Since Munn wrote, something has been learned of the behavior of wild rats, at least in semi-natural conditions. Accordingly, the next section is an account of their social signals, classified by the sensory modalities which they influence. Unless other sources are quoted, the statements in the next three sections are based on the observations of Barnett and his colleagues [37, 43, 45, 52]. Consult also J. P. Scott for a general review [594], and J. A. King for examples of the social behavior of non-murid rodents [367, 368].

5.2 SOCIAL SIGNALS

5.2.1 Tactile Signals

The signals on which we are best informed act through contact or vision. This is because they are the most easily studied by the microsmatic adult human observer with an upper hearing limit of about 18 kHz. We begin with an example which does not constitute a simple, well-defined stimulus.

Huddling is one of a number of ways in which rats derive cutaneous stimulation from each other. Soulairac has published a formal account of the familiar huddling behavior of laboratory rats. He allowed a group of four males and four females to live undisturbed in a large cage. Although there was opportunity to separate into isolated individuals or pairs, the rats slept together in a group. Only parturient females isolated themselves [630]. Similar observations have been made of wild rats in large cages. Adults, strangers to each other, are placed in an unfamiliar cage, which they explore in the manner described in § 3.2.1; but they also tend to group together (figure 34). Later, they sleep or rest in groups either in nest boxes or in the corners of the main cage. This behavior is not merely a product of the shelter or the tactile stimuli offered by these places: if rats do rest on the cage floor, they usually do so together in one corner; the chosen corner may vary, but the grouping remains rather constant. Similarly, when several nest boxes are available, only one or two may be occupied; when more than one, each is as a rule used by a group. Again, the choice of nest box may vary.

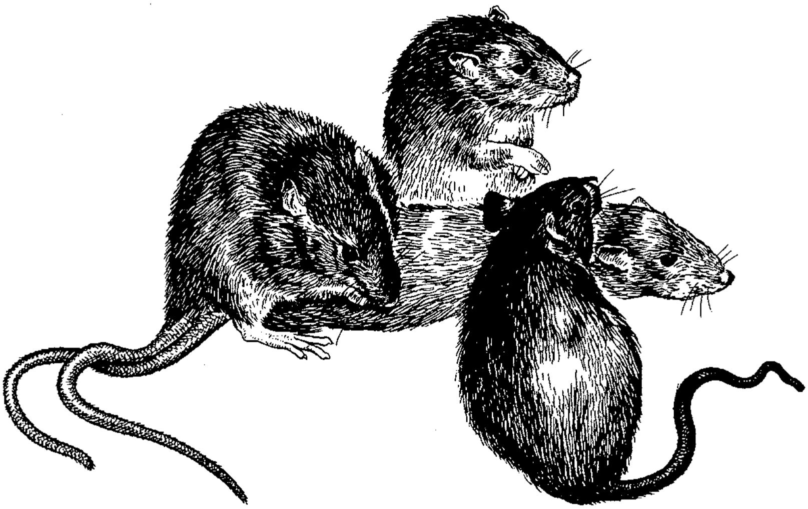


Figure 34. A group of wild rats. These rats had recently been put in a large, strange cage; they were strangers to each other. In the intervals of exploration they collected in groups of the kind shown. Three are *Rattus norvegicus*; the darkest one is *R. rattus* (black variety). (After Barnett [37].)

Huddling is often supposed to have a heat-conserving function. Certainly, the heat provided by other animals is sometimes important for small mammals, including rats [254] and mice [532]. Nestling rats especially depend on heat from their mother, since they cannot regulate their own temperature until they are at least eighteen days old [56]. The colder the environment, the more important an external source of heat becomes. Nevertheless, in ordinary conditions in the laboratory, huddling has no energy-conserving effect [83]; yet it still occurs.

Whatever the function (survival value) of huddling, we may guess that this behavior has a wider significance than its role in thermoregulation. In any case, it raises questions about the precise character of the stimuli to which animals are responding when they huddle together. The stimuli could include the temperature of the skin of other rats, the pressure of their bodies, or something less obvious. Laboratory rats (and undoubtedly wild rats also) are attracted to each other from a distance: in observations by Latané & Glass, rats not only approached each other in an unfamiliar arena, but tended to crawl under or walk over each other. They did not respond in the same way to inanimate objects or even to anesthetized rats [397]. Approach and making contact give the impression of being examples of what used to be called "innate" behavior (§ 9.2), but nothing is known of how the behavior develops: the earliest contacts of a rat with others are with its mother and litter-mates; in a rat's first environment, cutaneous stimulation from other rats is almost continuous. Whether this influences later huddling has not been investigated.

Huddling is an extreme form of herding. There are also more specific forms of tactile stimulation which seem to encourage approach or to discourage attack, but the exact roles of these performances are difficult to establish. Each signal presumably (i) reflects the internal condition of the performer and (ii) has a specific effect on the other; but statements on these conditions and effects are usually only guesses.

The most distinctive of these signals is *crawling under* (figure 35). This act, accurately described by its name, is performed by both *R. norvegicus* and *R. rattus*, and has been observed especially among males in situations which might lead to conflict. If a strange male approaches a non-aggressive male on the latter's territory, the resident may crawl under the stranger instead of attacking. A stranger may also crawl under a resident. This behavior is also seen among young rats during play. An obvious hypothesis is that, when it is performed by adult males, it inhibits attack, but there is no satisfactory evidence of its effect on the behavior of other rats. It might be questioned whether it is a social signal at all, for rats tend to keep in contact with surfaces; but males rarely, if ever, crawl under females, only under other males. A second act may, again descriptively, be called *walking over.* This too is evidently carried out as a specific response to the presence of another rat: rats often literally go out of their way to crawl under or walk over other members of their colony. They may also urinate on them [268].

A third type of contact is *allo-grooming,* so-called to distinguish it from self-grooming. This usually consists of a gentle nibbling of the fur on any accessible area of skin. Again, it is seen mainly in conflict situations (figure 36), but it is not confined to them. Interpreting this behavior presents special difficulties. It has been called an "amicable" act, that is, one which tends to diminish conflict. But sometimes allo-grooming takes a different form from that shown in the figure: the animal doing the grooming is above the other, and the animal groomed may be held down by a forefoot. This has been observed in the intervals between attacks. E. C. Grant even refers to "aggressive grooming" by laboratory rats [267]. A first step to understanding this behavior will be to establish correlations of allo-grooming both with the physiological state of the performer and with the performer's other behavior, such as threat; a third and still more obvious requirement is to find out just what effect, if any, it has on the rat groomed.

A fourth type of contact, about which we know even less, is *nosing,* in which one rat gently pushes with its nose at the flank, often near the neck, of another (figure 37). This is seen in a variety of situations, including that in which a female in estrus approaches a male (§ 6.1.1).

A last group of tactile signals result from *attack*: a rat leaps at another with rapid adductions of its forelimbs, and briefly bites at an extremity, often the tail or an ear (figure 38). Very rarely, biting is more severe. In the intervals between attacks, both animals may adopt an upright, "boxing" attitude, in which they face each other and each pats the other with its forepaws (figure 39). The behavior involved in clashes is further discussed below (§ 5.3.3).

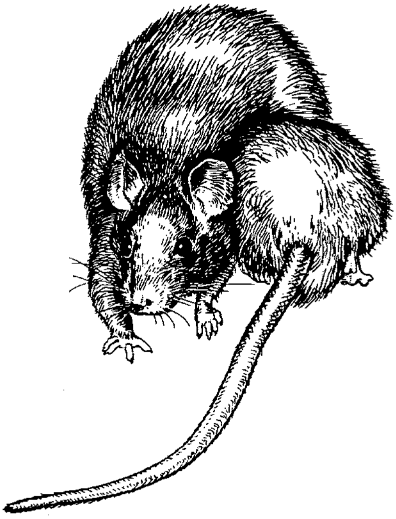


Figure 35. Amicable behavior. A *Rattus rattus* "crawls under" a *R. norvegicus*. (After Barnett [37].)

5.2.2 Visible Signals

The items now to be described are not sharply distinct from tactile stimuli, since they may be accompanied by actual contact; but they, especially the second, are distinctive postures and seem to have a primarily visual effect.

The first consists of *lying down* on one side with the eyes closed (plate 17), and is often performed, by both sexes, on the approach of another rat. It is observed quite generally among the rodents [52]. It has been called a "submissive posture", but such an anthropomorphic name is not very helpful. Although there is no quantitative analysis of this behavior, an animal which performs it can confidently be said not to have attacked the other, nor to be about to attack it.

The second signal is illustrated in figure 40 and plate 10: the flank is presented to an opponent; the legs are fully extended and the back arched; the performer may dance or prance round the other, or both may take up this attitude in contact. Calhoun seems to be referring to this behavior when he writes of "hip-throwing" [126]. It has also been called a "threat posture" [37], but this name was given without good evidence of its effects on other rats.

Since then, some correlations have been established. First, the relationship between the incidence of the threat posture and attack has been formally confirmed (figure 85). The readiness with which a male, settled in a cage or other territory, will attack a strange male is raised by the presence of females.

The figure gives an example, from observations on a single rat, of how posturing fluctuates with attack. When there is such a correlation, between different aspects of the behavior of the same individual, we may guess that the actions have to some extent a common physiology: the internal state (whatever it is) that predisposes an animal to attack, also increases the probability of threat-posturing.

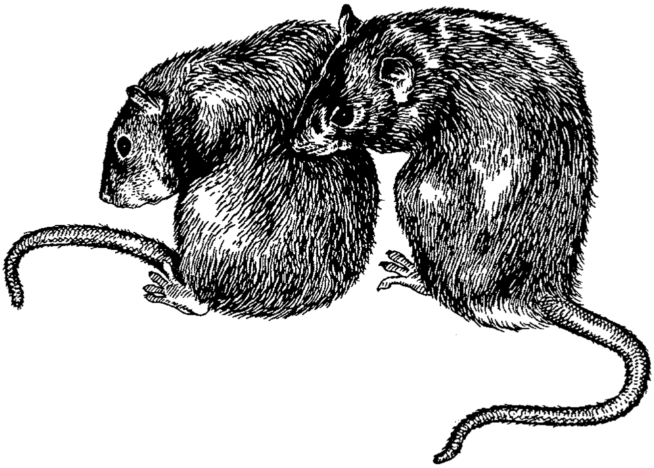


Figure 36. Ambiguous behavior. Grooming of one wild rat by another. The left-hand male was a newcomer, and was attacked as well as groomed. (After Barnett [37].)

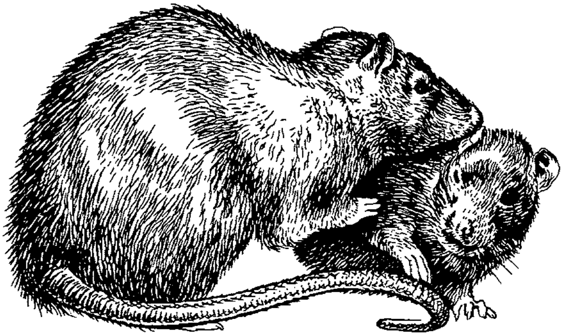


Figure 37. Amicable behavior. A male paws and nuzzles a female; the latter adopts a submissive attitude.

This positive correlation does not hold in all circumstances. Attack is influenced, not only by the attacker's internal state at the start of the encounter, but also by the characteristics of the opponent. One factor is size. In experiments in which a single caged resident male encounters another adult male, the greater the weight of the newcomer, relative to that of the resident, the greater the number of threat postures performed by the resident [45]. But the amount of attacking by the resident does not go up to correspond. One hypothesis is that, above a certain relative size, the newcomer's stature tends to inhibit attack by the resident, but this has yet to be proved. There are, no doubt, other properties of the opponent which influence the behavior of the potential threatener. Among them are the sounds he makes and the array of odors that he presents, as we see below. But there is no quantitative information on the effects of these other features.

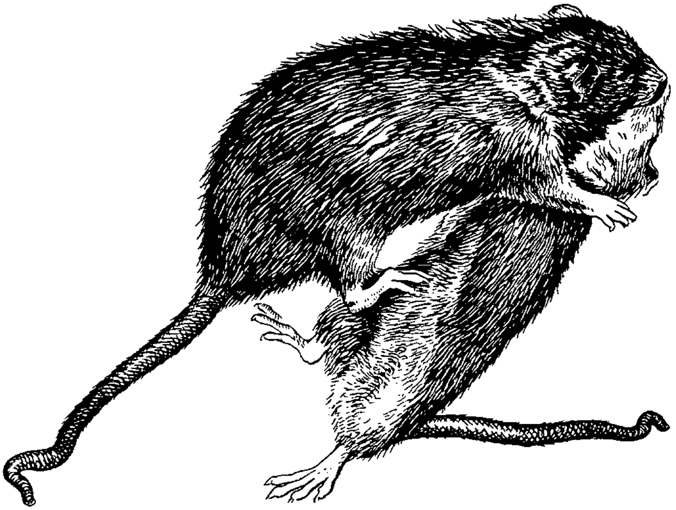


Figure 38. Attack. A fierce male attacks a strange male by leaping and biting; this movement is accompanied by rapid adductions of the forelimbs. (After Barnett [37].)

Postures which occur when attack might be expected are sometimes explained as being due to "fear"; they are also supposed to prevent "aggressiveness" (reviewed by Hinde [326]). If we say that a posture is due to fear, we need to know how to identify fear objectively in another species. In practice, when a clear definition is stated or implied, we find that a posture is said to represent fear when it is positively correlated with flight or withdrawal. This type of analysis is not applicable to the threat posture of wild rats, since the posture is not correlated with flight by the threatener.

We may, then, say nothing conclusive about the interacting internal states which underlie threat and attack. The effect of threat-posturing on other rats is also difficult to establish. The posture might (i) reduce the likelihood of attack by the opponent, or (ii) cause the opponent's withdrawal. There is evidence on the second hypothesis, based again on the observation of single resident males faced with intruders. In these conditions there was a strong positive correlation between the amount of threatening by the resident and the amount of withdrawal by the intruder, which emerged after the observations had been analyzed statistically [45]. For satisfying evidence of a *causal* relationship between threat and withdrawal we need still more evidence: it remains possible that the withdrawal was induced, not by the threat-posture itself, but by some other, correlated property of the threatener, such as odor.

Figure 39. The boxing position.

The threat-posture has been discussed at length because it presents, in a clear form, problems of method and interpretation which arise in the study of social signals generally. We return to these questions later (§ 5.6).

5.2.3 Olfactory Signals

The importance of the olfactory sense for most mammals may be inferred from a superficial study of their behavior and of the relations of the olfactory organs to the brain. The part played by smell in feeding and exploration has already been mentioned. Rats sniff all food and, indeed, all objects that they encounter; but they also sniff other rats, especially strangers and potential mates (figure 49; plate 9). They not only respond to odors, but also produce them; like other mammals, they have an elaborate equipment of glands which secrete olfactory signals. These substances are called pheromones.

Two groups of signals determine the manner in which one animal responds to another: both are concerned with recognition. (i) Hardly anything is known of species-odors, but we may guess that they exist among rodents (§ 5.5). We must not, however, also assume that responses to specific odors are irrevocably fixed for each individual of each species. As we shall see, social responses to the odors of conspecifics depend on the conditions in which the young animal is reared (§ 8.7.2).

(ii) The evidence of distinctive group or colony odors is more convincing When a strange wild rat is introduced into a colony, there is a marked increase in "recognition sniffing" among the residents. When an adult resident male meets an adult male intruder, the resident threatens or attacks in the manner fully described later (§ 5.3.4); fellow-residents are not attacked. Odor is the most probable means by which this discrimination is made, but there is not yet any satisfactory experimental evidence on wild rats. Krames & Shaw, however, have found good evidence of group discrimination by laboratory rats [379]. Similarly, J. H. Mackintosh & Grant rubbed male laboratory mice with the urine of other males. The mice so treated were attacked by companions with which they had previously been living peaceably [421]. Despite this finding, it is still possible that a rat or mouse put in a strange place secretes a distinctive odor which induces attack.

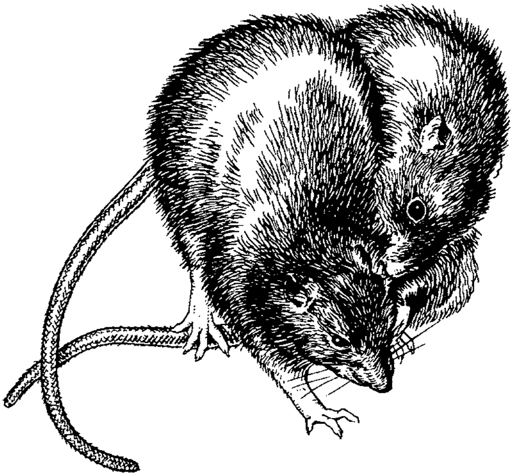


Figure 40. Threat posture. Two males of equal status both adopt the arched-back attitude. No fight followed.

An important characteristic of pheromones is that they can be effective in the absence of the signaler. Scent-marking is widespread among mammals [228]. Rats certainly leave odor trails during their movements about their living space. Where they run regularly over a light surface, they leave a dark, odorous, smear. According to Reiff, urine and genital secretions contribute to the odor trails, and the trails are followed by other rats [538]. Steinbrecher, in a detailed study, has confirmed the attractiveness of wild rats' "body-odor" to other rats [647].

Pheromones produced by females, especially when in estrus, are probably among those left as traces. Calhoun has watched wild rats in a large colony. He describes how females in estrus explore further than usual and leave their odors on objects over which they move. Males respond to these signs, and follow the females back to their burrows [126]. These observations suggest that males can distinguish the odor of receptive females from others. In confirmation, Le Magnen gave male laboratory rats a choice between a pathway with the odor of a female in estrus and one with the odor of a non-receptive female: the former was preferred [402].

Carr and his colleagues tested odor discrimination with the equipment shown in figure 41. Adult male rats approached a container with a female in estrus more often than a similar container with a non-receptive female, even though both females were protected by a barrier. This need not have been due to different odors: the females might, for example, have been making different sounds. In further experiments the containers merely had the odors of females in different states; and the result was the same. These findings refer to experienced males. Males with no experience of females, and experienced castrated males, did not make the discrimination. These workers also give evidence for an ability by females to distinguish the odor of a normal adult male from that of a castrate; previous experience and sexual receptiveness both contribute to this ability [143].

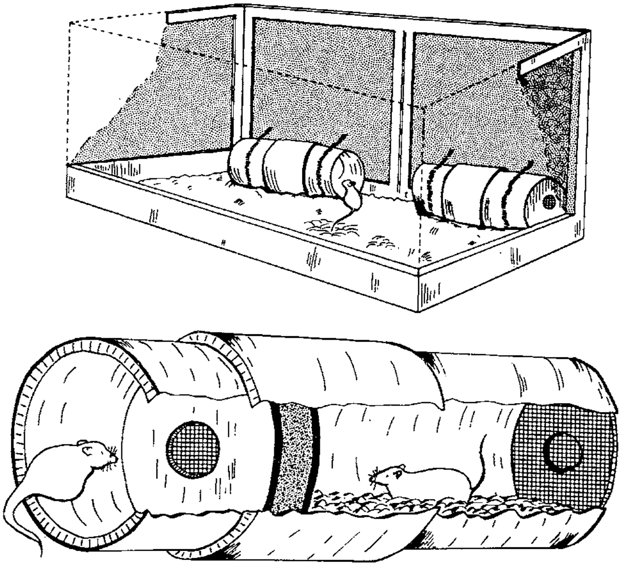


Figure 41. Testing for preference for odors. A rat (above) has the choice between two containers. Below, a female in the container is inaccessible but can be smelled. (After Carr *et al.* [143].)

The effects of castration are, however, evidently complex. Carr & Caul recorded the responses of rats in the apparatus shown in figure 42. They found it possible to *train* both normal and castrated males to distinguish between the odors of receptive and non-receptive females. Similarly, both normal and spayed females were trained to discriminate between the odors of normal and castrated males [142]. Hence, while a castrate displays no initial preference, it can still discriminate these odors.

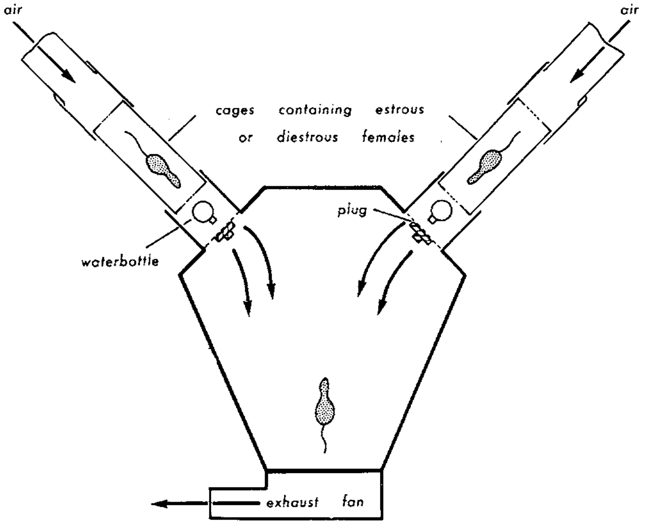


Figure 42. Test for olfactory discrimination: a male is required to distinguish a female in estrus from one in diestrus by odor alone. Continuous noise drowns audible signals. (After Carr & Caul [142].)

There are probably other odors which reflect an animal's momentary state. There is evidence, to be discussed later (§ 8.2.4.1), of odors which indicate success or failure in finding, for instance, food; and both rats and mice seem able to distinguish the odors of "stressed" from "non-stressed" conspecifics [144, 691]. The odor of an attacking or threatening rat may also differ from that of a peaceable one, but this is only speculation.

One group of pheromones has no direct influence on approach or withdrawal by the recipient. They act on the estrous cycle or on the implantation of embryos in the uterine wall, and are mentioned further below (§ 5.3.1). Finally, the odors experienced by a mammal early in life may influence its later behavior, especially in social situations. These, too, are discussed later (§ 8.7.2.1).

5.2.4 Sounds

The squealing or squeaking of rats, though easily heard, has only recently been studied in detail. Even now, knowledge of the noises made by *R. norvegicus* is very incomplete. Their social effects are evidently of several kinds. First, nestlings, especially before they become active, squeak a great deal. According to Wiesner & Sheard, infant laboratory rats probably make most noise when their stomachs are empty or when their skin temperature falls below a certain level. The effect of temperature is important when a young rat has strayed or fallen from the nest: the mother responds by retrieving it [714]. More is known about the squeaks, including those above the human range (ultrasonic), of infant laboratory mice. Cooling certainly induces them to utter sounds that influence parental behavior. Of the calls they give, one kind makes the parents attend to the young; another kind, or perhaps greater intensity of calling, makes adults withdraw or behave in an agitated manner [82, 502, 507].

Among the sounds made by adults is a gentle piping or whistling. C. S. Evans, in unpublished work, has recorded duets during encounters between wild male *R. norvegicus*: on one occasion one of the animals had a call of fundamental frequency of about 2,100 Hz, with harmonics; the other had a fundamental frequency of about 2,600 Hz [45]. Probably, this type of sound is made more often by a male when threatened or attacked, than by an attacker: it is heard from males defending a nest against a visitor, and it seems then sometimes to be an effective deterrent without further action by the defender; but this has not been firmly established. Females, too, make this sort of noise, when they defend a nest containing young; they also make it when approached by a strange male. In these situations the whistle may again inhibit approach or deter attack, but these effects have still to be shown experimentally. Similar but more detailed observations have been made on *R. fuscipes* [63].

A third kind of noise is the scream known to anyone who has handled wild rats. On hearing it, other rats take cover. It is probably an alarm call of the sort heard from many other species. To the human ear, *R. norvegicus* and *R. rattus* have very similar screams. This accords with expectation since, as Marler has shown, alarm calls of different species of birds are similar [436]: they are difficult to locate, and there is no advantage in their being species-characteristic, as there is for a sexual signal. A second social function of the scream is in defense. A rat defending a nest against a visitor, or approached by another rat while on strange ground, may turn from whistling to screaming. The noise probably also has a non-social function, since it tends to deter predators: it is certainly disconcerting to man. Screams, too, have been recorded from *R. fuscipes* [63].

A fourth noise, tooth-chattering, made by male rats, is also characteristic of many other species of rodent. It is mentioned again below (§ 5.3.4).

The exact social effects of the sounds made by adults are easily guessed at, not easy to decide with certainty. It is misleading to describe them as discrete signals. Like the postures described above (§ 5.2.2), they vary greatly; "scream-whistles" and "whistle-screams", are common. There are also ultrasonic components [599]. Moreover, they are accompanied by visible signals and perhaps also by the secretion of pheromones, all of which presumably combine in influencing the behavior of conspecifics.

5.3 TERRITORY AND DISPERSION

5.3.1 Populations

In favorable conditions, wild rats live crowded together in colonies which may number many hundreds. Although herding is of obvious importance, much more attention has been paid to dispersive behavior, not only of rats but also of other species. Perhaps this reflects the preoccupations of the observers. The first accurate information on rats came from studies of populations [43]; these in turn arose in part from the practical importance, for pest control, of a knowledge of the dynamics of rat numbers.

When most members of a settled rat population have been killed, the remainder breed more quickly and numbers soon rise again. The same type of population growth is observed if a few rats colonize a favorable environment for the first time. At first the growth rate is high, but later it declines, sometimes quite smoothly, until a maximum is reached. Thereafter, if the environment remains unchanged, the rat population may be steady. The environment, in this context, includes predation by men, cats, dogs, hawks and others. An example is given in figure 43. This refers to a sewer population; rats in a more complex and heterogeneous environment would probably yield a more fluctuating curve. But, whatever the environment, every rat population, like that of all other species, stops growing at a certain point. What determines the maximum? Where a fairly steady population is maintained, this seems usually, if not always, to be due to the operation of factors which act with increasing intensity as the population grows. Such agencies are said to be density-dependent or density-related. This notion, reviewed by Lack [386] and by Andrewartha & Birch [18], is not as simple as it seems at first; but it makes a convenient frame of reference for talking about rat and many other populations.

A factor which might be supposed to act in this fashion is food. Consider a habitat in which the food supply is constant: for example, in an area in which rats feed on garbage or sewage, the daily rate at which food becomes available might vary little. If a few rats entered such an area, their numbers would at first increase slowly, later rapidly, until eventually the curve would flatten to a maximum. This maximum must either be determined by the food supply, or remain below the level at which the food supply becomes inadequate. Other potentially density-related factors are the available nesting places (especially important for the rearing of young), predation, and infectious disease.

This formidable group of adverse environmental features might be thought enough to restrain any population. Nevertheless, there is increasing evidence that none can account for the control of at least the populations of mammals, and that social interactions must be invoked if the facts are to be explained. Chitty and his colleagues have made a long, detailed study of the population dynamics of a vole, *Microtus agrestis,* in Wales [153]. This is one of the species which fluctuate in numbers with some regularity. The populations of voles rise in the manner described above, but do not remain steady at the maximum: instead, they crash, usually at intervals of four or five years [218]. Typically, the crash occurs before the food supply has been over-eaten. No evidence has been found that predation or infection are important. Ranson [536] had bred voles of this species in the laboratory, and had observed violent conflict between adult males, later described in more detail by Clarke [158].

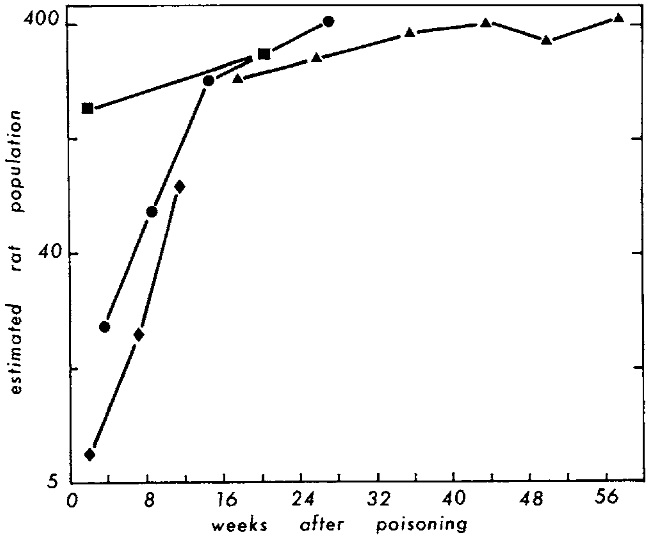


Figure 43. Growth of sewer rat population after reduction by poisoning. Estimates of numbers were based on census baiting (see text). Recovery from the lowest figure was too rapid to be due to breeding alone: immigration into the emptied living space must have played a part. (After Barnett & Bathard [48].)

Accordingly, Elton proposed an important hypothesis: "This social antagonism among voles probably exists in nature, and may be very important at different levels of population, and may prove to explain some of the mortality at higher numbers" [218]. The hypothesis became prominent with the finding that, as Chitty wrote, "declines in the numbers of voles can take place even though the environment seems favorable" [152]—a conclusion that was indirectly supported in later observations, including some of a dramatic crash wholly without evident cause [499]. A more direct test has been described by Turner & Iverson. They observed a population of *Microtus pennsylvanicus*. Males were trapped at regular intervals during seventeen months, and put together in pairs for ten minutes each. Intolerant behavior, such as threat, was most intense during the two breeding seasons covered, but a relationship with population density was not found [687]. In this kind of work it is difficult to separate the apparent effects of seasonal changes (which include a cycle in the secretion of male hormone) from those that might be due to crowding.

Further evidence comes from non-cyclic species, that is, those with a more usual type of population dynamics. Snyder studied two natural populations of the woodchuck, *Marmota monax*, in a region where there was never shortage of their plant food. Removal of a substantial proportion of a population was followed by a higher pregnancy rate among young females, a raised survival rate among the young, and a rapid return to the original density. These observations, and others on the movements of individuals, suggested the existence of a "density-dependent adaptive mechanism" which controlled the growth of the population [627]. Sadleir has described changes in a population of a deermouse, *Peromyscus maniculatus.* He observed interactions among males at different seasons: in the breeding season hostile behavior was more frequent than at other times; and there was a correlation between mutual intolerance and the seasonal decline in the density of the population. Laboratory experiments also revealed an accompanying intolerance of males towards juveniles [573]. Healey drew similar conclusions from field experiments on this species: deermice which were driven out of their area as a result of social intolerance were not directly injured, but some died through failing to find a suitable place to live [302].

A further development has come from a suggestion by Chitty that, as fluctuating populations alter in density, they change genetically as well as in behavior [153]. Krebs and his colleagues have studied two North American species of *Microtus,* in a long series of experiments. Their findings emphasize the importance of the dispersal of these animals, resulting from emigration during the phase of rapid increase in numbers. Populations allowed to grow in fenced areas, each of 0.8 ha, reached exceptional densities and so over-ate their food that signs of starvation appeared. Evidently a normal process of dispersal had been prevented. When, in other experiments, dispersal was allowed, two polymorphic serum proteins were used as markers, to test for genetical variation. The emigrant populations then proved to be genetically unlike the stay-at-homes: that is, gene frequencies at the two loci studied were markedly different. The relationship between genotype and behavior has still to be found out [380]. This work represents a notable new development in a difficult region of study. The method could be applied also to species that exist in very different population densities, but do not fluctuate regularly.

We may now return to rats. Calhoun added strange *Rattus norvegicus* of both sexes to established urban populations. When he retrapped some weeks later, only 16 percent of the foreign rats remained: the rest had either died or emigrated. The indigenous rats kept to their usual, quite small, home range, whereas the foreigners moved widely [123]. A second study by Calhoun was of a single large colony (figure 44). Rats living near the single source of food molested those living further away, when the latter were moving between the feeding point and their nests. Before the population had reached its maximum, there was evidence of conflict, though not specifically for food. The amount of persecution suffered by different groups of rats was reflected in differences in growth and fertility. Rats, in fact, defend an area around their nests against other members of their species: they are territorial animals, as further discussed below (§ 5.3.3).

Schein & Orgain studied rats with access to a food supply (garbage) much in excess of their needs. They, like Calhoun, suggest that the distribution of the food in the biotope is important in determining population density [513, 580]. Perhaps rat populations are sometimes kept down by intraspecific conflict interacting in a complex way with the distribution of food and shelter. Unfortunately, as A. Watson & Moss point out, this type of interaction has not yet been effectively analyzed [703].

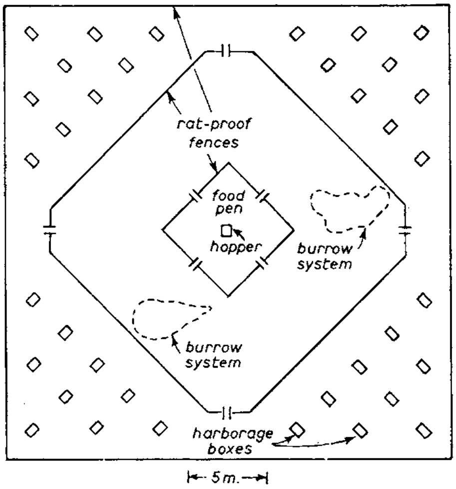


Figure 44. Experiment on social behavior of *Rattus norvegicus.* The only food available was in the center of the enclosure. Rats living in the peripheral areas were attacked on their way to food and had a higher mortality and were less fertile—an example of territorial behavior and its effects. (After Calhoun [124].)

The simple model of rat populations rising on an "**S**-shaped curve" to an asymptote clearly needs to be tested against actual findings on natural populations. Fortunately, the difficulties of making reliable estimates of rat numbers have been overcome in a few studies, and some have shown that rat populations do increase at a declining rate to a maximum. Urban populations have been described by D. E. Davis [185], and by Emlen and his colleagues, on the basis of the study of signs of rat activity [220]; rural populations, as already described, have been reported on by Barnett and his colleagues [49]; and sewer rats by Barnett & Bathard [48] and by Bentley and others [84, 85]. Sewers represent a rather simple environment, for there are few relevant species and the food supply is usually maintained at a steady rate; hence census baiting can in favorable circumstances reveal the expected type of population growth (figure 43). Nevertheless, sewer populations are not isolated from the surrounding populations: when large numbers of sewer rats are killed, numbers are restored not only by breeding but probably also by immigration from the neighborhood [48]. There are other reasons why the model of a closed area with constant amenities and a ceiling population can be misleading. The area occupied by rats often increases with a rising population; further, new ground may be colonized *before* the maximum density is reached [49]. The extent to which this is due to exploratory behavior alone is not known but, although exploration must play a part, social interactions probably also contribute to dispersal.

The physiology of "social stress" is discussed below (§ 5.6.3) and in § 10.2, but one aspect must be examined now. Crowding and intolerant behavior can lead, not only to dispersal of a population, but also to lowered fertility: social interactions may regulate density primarily through their effects on breeding

[43, 155]. D. E. Davis has reviewed studies of commensal populations of *R. norvegicus*, in which increased pregnancy rates were recorded when populations were brought below their maxima by trapping or poisoning [185]. Similar observations on woodchucks have already been mentioned.

Such observations, though interesting, do not tell us how fertility is altered by changes in density. In very crowded conditions in captivity, female domestic mice sometimes seem to neglect their young owing to repeated disturbance [43]. But there is now beginning to be evidence that more subtle density-related factors influence fertility. If a female house mouse, *Mus musculus*, is inseminated, and is exposed to the odor of a strange male shortly thereafter, the embryos usually fail to implant. This phenomenon, pregnancy block or the "Bruce effect" [116, 117], has been described in *Peromyscus* as well as the house mouse. It may reduce fertility in natural populations when they increase beyond a certain level; but on this everything remains to be found out.

5.3.2 Conditions for Conflict

We now return to direct studies of behavior. To establish a stable, healthy colony of wild rats, it is best to begin with a group of sexually immature individuals; or a single adult male with one or more females may be used. In either case conflict is very unlikely [37].

By contrast, a clash is highly probable when an adult male enters a region where another has settled. This holds even if the resident male has been reared from birth only with its mother and siblings, and consequently has never encountered a newcomer before. Small artificial colonies have been studied in large cages, some only of adult males, some of males and females, some of family groups. Putting adult males in such colonies usually leads to their death. (There is no corresponding mortality among the residents; nor do rats die if put in such cages alone.) Similar observations have been made of males put in a cage containing only one resident male. By contrast, the addition of females rarely results in harm to them. Attacks on young rats do not occur [37, 51, 227].

These observations suggest that conflict is a consequence of occupation of a territory, but they do not prove that intolerant behavior is always territorial. People may say: perhaps males sometimes fight "spontaneously" among themselves, or even for a female. Males brought up together from youth do not come into conflict; and even adult males, strangers to each other, put together in an artificial colony may live peaceably with each other. For this to happen, they must all initially be strange to the cage or enclosure, and they must all be introduced at the same time. Even an interval of ten minutes between one male and the next may lead to conflict; evidently a male introduced early establishes itself very quickly as a resident. Provided these conditions are satisfied, all-male colonies of *Rattus norvegicus* (or *R. rattus*) may be maintained indefinitely. In a settled colony, a serious clash between males is unusual, even in a quite dense laboratory population. Hence crowding is not by itself a cause of conflict among wild rats [37].

There is next the question whether males fight for females. Colonies containing both males and females have been compared with others containing only males, and with mated pairs in small cages. While the all-male colonies were peaceful, in the mixed colonies deaths among the males were the rule: in two extreme instances all except one died. There were few deaths among the females, and there was no evidence that these were due to fighting. Nevertheless, direct observation showed that there was no fighting for females. When a female is in estrus, the males concentrate on copulating with her; there is no competition, and the female accepts any male indiscriminately. (This is a general phenomenon among mammals.) When a female is not in estrus she is usually ignored; but, during the period preceding estrus, males sometimes sniff her genitals or attempt coitus unsuccessfully. The significance of the greater conflict, injury and death in the presence of females is discussed in § 10.3.

The preceding paragraphs refer to adults. There is no evidence that active, sexually immature rats are ever threatened or attacked. They play in a lively fashion, crawl under, box, and wrestle with each other without any sign of trauma. They also run over and under adults (and follow them, as described in § 4.3.3). At the age of about four months, wild males display a marked set of changes. This is the period loosely called "puberty" (reviewed by Bronson & Desjardins [113]). It occurs earlier in laboratory rats. At this time, as we know from study of laboratory mammals, the amount of androgenic hormone in the blood rises, the testes complete their descent into the scrotum, and the adult patterns of herding and intolerant behavior appear. Castration substantially reduces the intensity of intolerant behavior; testosterone largely cancels the behavioral effects of castration. Testosterone can also hasten male puberty.

Since much of the preceding account concerns animals kept in large cages, it may be asked whether some of the behavior is abnormal as a result of captivity. Fortunately, both Calhoun [126] and Telle [669] have observed similar behavior and social effects in less confined or unconfined colonies. Study in the laboratory has the advantage that animals can be identified as individuals, and their conduct reliably and quantitatively recorded. The ideal is to combine field and laboratory studies.

5.3.3 Territory

The attacks by resident rats on strangers, in the experiments described above, are examples of territorial behavior. By a territory is meant a region defended against members of the occupants' species. Among wild *Rattus norvegicus*, territorial behavior is, except in one type of situation, probably as a rule a prerogative of males. The exception is the behavior of females with young nestlings, when the defense is only of the nest: lactating females may defend their nests against all visitors, regardless of age, sex or familiarity; but the intensity of nest defense varies, for some females allow adult members of their colony, of both sexes, to share their nest with the young. The two kinds of territory are common among mammals. Female *R. norvegicus*, in the most closely observed experiments, took no part in defending any larger region, and males defend a nest only when cornered in one by another male.

These statements are based principally on observations on trapped rats in large cages in the laboratory [37, 45], partly on the work of Calhoun already cited [126]. Telle has observed similar behavior in natural populations. The *Rattus norvegicus* that he studied defended only the pathways in their living space; but, unlike previous observers, he recorded attacks on female intruders, as well as on males. He also describes the behavior of *R. rattus*: this species he finds defends the whole of its range. Perhaps the difference is related to the different habitats occupied by these rats: *norvegicus* burrows and moves largely on the ground; *rattus* is a climber. The intensity of territorial defense by *norvegicus* evidently varies with the size of the population: large groups, according to Telle, are less territorial, and admit strange rats more readily than small ones [669].

What effects has territorial behavior on the species which display it? At first sight it seems dysgenic for animals to come into conflict with members of their own species. If species have evolved by natural selection, their social behavior should be co-operative. The apparent anomaly is partly resolved when we realize that territorial encounters are rarely directly harmful. Behavior that we are tempted to call "aggressive" usually consists of displays which lead to the withdrawal of the intruder. Even the violent features of the clashes of confined wild rats seldom lead to serious wounding. These features of the social behavior of animals have been emphasized by ethologists for at least two decades, for instance by Tinbergen [678], but they are still not always understood. Men are often dangerously belligerent. Perhaps some of them project their own feelings on to other species, which are then described as violent or aggressive. This misleading anthropomorphism is sometimes coupled with the notion that territory among animals is the same as property-holding by human beings.

Unlike human properties, the territories of each animal species are rather uniform in a given type of environment. Property-holding by human beings is diverse, but territorial behavior of other species is stereotyped. Since territorial behavior is widespread, we must assume that it contributes to the survival of the species in which it occurs. The effect of territorial behavior is undoubtedly to disperse individuals or, more usually, pairs and their young or larger groups. This prevents increase above a certain density. Perhaps it ensures that some individuals or families live in optimum conditions, even if others, driven from favorable environments, die or are made infertile. We still do not know whether dispersal has its principal effect by maintenance of the food supply, by avoiding infectious disease or by allowing undisturbed breeding. All these hypotheses have been proposed, and others also [43]. The problem remains of testing them effectively.

5.3.4 Motor Components of Attack

Among rats, as among other animals, the behavior commonly called "fighting" is an example of a stereotyped behavior pattern with a number of distinct components. In a typical encounter between a resident and a stranger, the components are all displayed by the resident: the attacked rat may adopt a defensive posture (figure 45), it may squeal or run away, but it does not fight back. In fact, the term "fighting" is another misleading anthropomorphism: "assault with battery" is more appropriate.

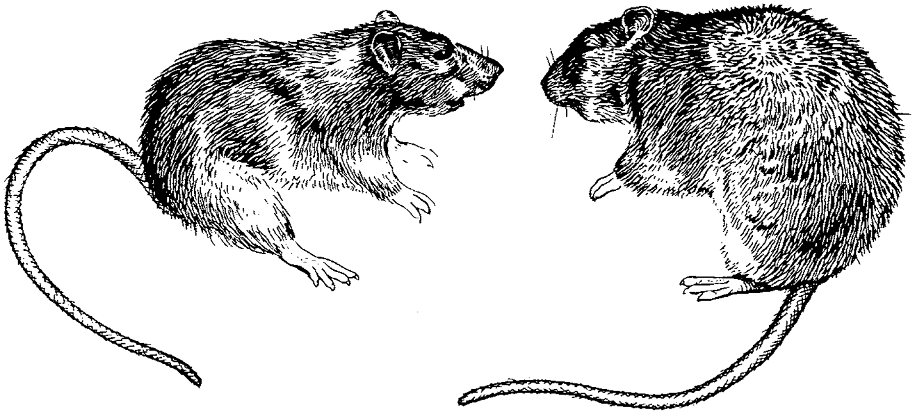


Figure 45. Attack. Attacker (right) and attacked newcomer both momentarily in a defensive position. The attacker has raised hair. (After Barnett [37].)

The first activity performed by a resident is often *tooth-chattering*. This is not confined to *R. norvegicus: R. rattus*, and other rodent genera such as *Cavia*, display it. It continues while the rat remains immobile after it has detected the presence of an opponent, and during approach. Its significance is unknown. It may act as a deterrent which prevents further approach by a stranger, but this is only speculation.

As a male about to attack advances, it urinates and defecates, and its hair is raised. In at least one species of the Murinae, the crested rat, *Lophiomys ibeanus*, the raised hairs of a disturbed animal reveal a striking pattern of black and white [174, page 219]. This perhaps has a deterrent effect on rivals. There is no experimental evidence that pilo-erection is a visual signal for *Rattus*, but it certainly increases the apparent size of the performer.

Typically the next stage is initiated by adoption of the *threat posture* by the attacker (plate 10; figure 40). This has already been fully discussed. In a complete sequence it is followed by *leaping* and *biting*. The attacker springs in the air and comes down on its opponent with rapid adductions of the forelimbs (figure 38); it also bites, often an extremity, but as a rule only very briefly. Rarely, very energetic *norvegicus* males bite and hold on. The leap is usually followed by a few seconds of violent movement by both rats, until they become disoriented (figure 46). All this can be followed in detail only by study of film taken at high speed. Such brief, violent bouts are followed by longer intervals in which both rats may adopt a stance as if boxing (figure 39). They may even huddle together, and the attacker may groom its victim in incongrouously peaceful fashion.

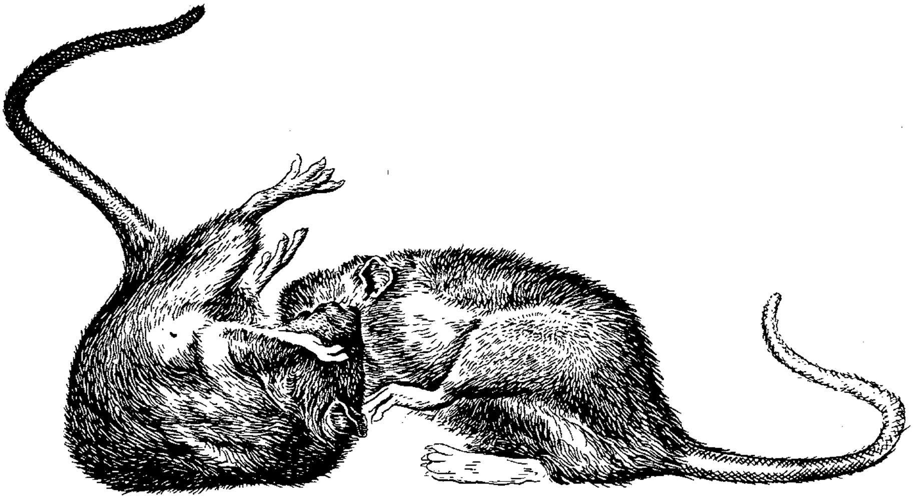


Figure 46. Attack. Both fall.

An account of such a complete sequence of actions might suggest that the different motor components of the total pattern are related to each other in a highly specific way. This is not the case: tooth-chattering, threat-posturing, leaping and biting, boxing and grooming may each occur independently of the others; there is no fixed chain or "hierarchical organization" of the components of the intolerant behavior of wild rats. The behavior is, indeed, extremely variable. Individual rats differ greatly in the intensity with which they threaten or attack, and in the extent to which they perform the separate motor patterns. This variation increases the difficulties of quantitative studies of the behavior.

5.3.5 Status

Much of this chapter is based on observations of rats in small, artificial colonies [37, 45]. By analogy with other mammalian species, and with birds, when such colonies are stable, a form of status system ("dominance hierarchy") might be expected, at least among the males. Such systems have attracted much interest among students of social behavior, once again perhaps because of analogies with our own species. In the simplest case there would be a dominant or top rat with prior access to females, food and shelter; a second rat would give way only to the first, and so on. In fact, nothing quite like this has ever been found. Rats brought up from before sexual maturity form, as we say, a group without conflict or any marked status system. When adults are put together, and conflict occurs, the relationships between the males are determined by the results of the clashes. Three types of males may be distinguished. *Alphas* are always large by comparison with others: in no instance has a rat been seen to defeat another *colony member* much larger than itself (though *newly introduced* rats of considerably greater weight are usually defeated). Alphas move about without hesitation or any attempt to take flight from other rats. They are the only rats that attack.

Secondly, *omegas* are the result of defeat by one or more alphas. Such rats flee at the approach of an alpha. In confined colonies omegas, after a day or two of persecution, are marked by their slow movements, drooping posture and bedraggled appearance. They lose weight, and die if not removed. A third category is needed for rats which, after defeat, adapt themselves to an inferior rôle: they have been called *betas*. They endure defeat and succeed in feeding with enough freedom to gain weight. Omegas and betas associate together without conflict: no "hierarchy" develops.

There was no uniformity in the numbers of alphas, betas and omegas in the small colonies studied, but in conditions of intense conflict there were fewer alphas and often only one.

In unconfined colonies, adult males probably vary in status from alpha to beta (in the terminology used here); any rat with an omega status would soon die or emigrate. The observations of Telle [669] on natural populations, though not detailed, conform with this. The function of status systems is presumably to prevent dysgenic conflict. Among wild rats, harmful intolerance is evidently prevented, for the most part, not by the setting up of a status system but by inhibition of conflict between members of a single family or similar group; the inhibition is perhaps strengthened by the various types of "amicable" behavior. Attack is usually released only by the arrival of a strange male; and this conflict promotes dispersal.

5.4 LABORATORY RATS

The preceding account will perhaps be strange reading for those whose only experience has been with laboratory rats. Munn, in his valuable compilation, relegates the account of social interactions to a chapter on abnormal behavior [490]. Another psychologist of distinction has remarked that rats have "very little social life" [682, page 229].

A few independent authors have paid some attention to laboratory rats as social animals. Small, at the end of the nineteenth century, before rat psychology had properly begun, made some reference to social interactions, but his main interests were in habit formation and in the ontogeny of behavior [618–19]. Buytendijk, in 1931, tried to break away from what he regarded as the unnatural situations inflicted on rats in mazes: he used a spacious observation box stocked with a variety of objects and giving scope for social encounters. Unlike most of the conventional workers of his time, he put much emphasis on exploratory behavior, but the conditions of his experiments did not facilitate the study of social behavior [121]. In 1952 Soulairac published a short description (already cited) of the effects on behavior of keeping laboratory rats in a group in a large cage with nest boxes. He observed their huddling tendency, defense of the nest by parturient females, and a decline in the readiness with which the rats accepted handling [630]. Calhoun, too, has described the huddling of crowded laboratory rats. He also observed much atypical social behavior among rats in extremely high densities [125]; this presumably reflects the many generations of selection in the laboratory, with loss or distortion of the normal responses to conspecifics.

In other studies, laboratory rats have been put in situations contrived to evoke specific forms of behavior. Seward sought to establish a "dominance hierarchy" by arranging bouts of "fighting" between pairs of males. No true "hierarchy" emerged; but past experience during clashes had much effect on subsequent responses to a stranger [597]. Similarly, E. C. Grant isolated adult male laboratory rats for ten days, and then observed them in encounters each of fifteen minutes. He classifies their postures in detail, and interprets them in terms of two main "drives": these are named "aggression" and "flight"; he also describes the rats as displaying "social drive" [267]. Grant's system of postures is the most detailed available, and can be used also to describe the behavior of wild rats of any species. The value of the general terms he uses is more debatable. The concept of "drive" is discussed later (§9.3, 10.3).

Much current research on the social activities of laboratory rats emphasizes intolerant interactions, usually under the heading of "aggression"; but the work of Latané and others provides an exception. They tested the effects of isolation on the "sociability" of albino rats, measured by the amount of time two individuals were in "direct physical contact": this could include anything from huddling together to a violent clash. But these albinos did not fight: they chased, sniffed and crawled under and over each other. Their behavior gave the impression of being playful and inquisitive. The main finding was an increase in sociability, as defined, among the isolated individuals, compared with controls kept in pairs [398]. In these experiments, the behavior of the isolated rats was evidently very different from that of the isolated rats and mice described below.

Among the problems which arise from observations of laboratory rats is the precise scope of the differences they display from wild rats. This can be determined only when the two kinds of rat are observed in identical conditions. A beginning in this field was made in a short study of albino rats which were put in conditions in which wild rats (as described above) had already been observed. Certain of the behavior patterns of wild rats, such as the threat-posture and crawling under, were in this case completely absent. "Fighting" resembled the wrestling of immature or female wild rats, not that of adult males. Newcomers put in established albino colonies were soon absorbed; none died. These newcomers did, however, lose weight and develop enlarged adrenal glands [42]. But the loss of weight at least may have been due merely to the disturbance of transfer to a new cage: Steinberg & Watson have reported diminished growth among laboratory rats due to disturbance only [646].

The laboratory rats whose social behavior is described in the preceding paragraph had, before they were observed, been kept in groups in small cages. It is probably important that they had not been kept in isolation, nor allowed to run freely in a complex environment. The extent to which laboratory rats fail to behave like wild rats depends not only on their genotype but also on the conditions in which they have been kept and the circumstances in which they are observed. Among the extreme treatments applied in laboratories to rats, mice and other species, are prolonged isolation, and electric shock to the feet. Both increase the probability with which an animal will attack, or at least jump at or wrestle with, a conspecific. Hence the confusing terms, "isolation-induced aggression" and "shock-induced aggression" have come into use. Rats kept alone for several weeks may respond abnormally not only to other rats [237, 257] but also to the experimenters, whom they bite. They have heavier adrenal glands, and develop altered resistance to poisoning and other insults. Similarly, a formidable syndrome of pathological changes, external and internal, have been described in laboratory mice kept in solitary confinement. Among them are skin lesions, which may have been due to the absence of grooming by other mice [243], but also abnormalities in the kidneys and other organs [33, 300, 692].

The biological significance of the isolation syndrome is not clear. The same applies to the violent biting and other behavior induced by shock (reviewed by Ulrich & Symmanek [688]). It does not closely resemble any normal social interaction. Wild rats, at their most violent among themselves, are more specific: they do not as a rule bite anything except their opponent, and they may not bite even him. Shock-induced violence perhaps more closely resembles the response to being seized by a predator (§9.3.3.1). Unfortunately, it would be difficult to put this notion in a form precise enough to be tested experimentally. In rather crude physiological terms, the behavior suggests a low threshold of arousal (§2.5).

Although we know that laboratory rats are unlikely to attack conspecifics with the vigor displayed by wild rats, there is only meager information on how they respond to being attacked. They might be supposed to be defenseless when faced with an attacking male wild rat, but they are not. The attacks, as we saw, usually consist, even at their most violent, of leaping and brief biting: they are not directly lethal. Laboratory rats put in a strange cage with a resident wild male may not evoke typical attack; but, if they do, they tend not to respond at all: instead of showing the signs of disturbance observed in wild rats, they may continue their exploration of the cage. The same behavior has been observed in rats of the second generation derived from a cross between wild and laboratory rats. It is a remarkable sight to see a laboratory or hybrid male moving slowly around a cage while a resident wild male vigorously postures or leaps at it without producing any evident alteration of behavior [47]. Boreman & Price have published a quantitative analysis of interactions between wild, hybrid and domestic rats; they describe the domestic rats as dominant over wild rats [103]; but, in the absence of an account of actual behavior, it is uncertain whether the encounters they observed resemble those between dominant and subordinate wild-type males. There is scope here for researches in which descriptions of the minutiae of behavior are combined with both quantitative and physiological analysis.

We may now summarize the behavioral differences, due to selection in laboratories, of our domestic rats from their wild cousins. First, some components of threat, attack and also of tolerant approaches have been lost or greatly attenuated. Most experimenters prefer rats which do not attack others, and such individuals have doubtless been selected for breeding. The loss of certain non-belligerent actions is not so readily explained and deserves further inquiry. Second, what "fighting" behavior remains is usually immature in character and rarely produces ill effects. Whether the lack of ill effects is due to its apparent feebleness is not known. Nor do we know whether laboratory rats secrete the same pheromones during encounters as wild rats. Third, wildness (running away) and savagery toward man (biting) have been almost lost. Fourth, Karli has described how the tendency to attack smaller animals (predation) has been much reduced [353]. The extent to which all these changes are necessary concomitants is uncertain. Fifth, and finally, avoidance of new objects in a familiar environment has been lost (§3.3).

It must not be assumed that other species will respond to domestication in the same way. Karczmar & Scudder find laboratory mice, *Mus musculus*, to be *more* combative than wild house mice of the same species [352].

There is still open a great field of inquiry in the physiology and genetics of rodent behavior. One question concerns differences in sensory acuity. Ralls has remarked on the high incidence of sensory deficits among laboratory mice, and the ways in which such deficits can lead to conclusions which do not apply to the species generally [534]. The same may apply to rats. A further problem is the sequence of events when wild rats are domesticated. H. D. King bred from trapped *Rattus norvegicus* for fourteen years, and mentions a very gradual loss of what she calls "obnoxious traits"; these include wildness and social intolerance [366]. More rapid changes were recorded in greater detail by Barnett & Stoddart. They compared trapped males with rats which had been bred in the laboratory for six to nine generations. The latter hardly attacked other rats (figure 86), but instead displayed much aberrant behavior, such as sexual mounting and huddling with newcomers.

These observations illustrate a general principle, that animals come to differ from their wild forebears after only a few generations in captivity. The findings do not, by themselves, however, distinguish decisively between genetical and environmental effects. The rats bred in the laboratory had been in cages all their lives, while the trapped rats had been born and reared in the free-living state [64]. But wild rats of the first three generations in captivity, observed in a previous study, behaved like those that had been trapped [37], and so a genetical change is the probable cause of the alteration in behavior. Nevertheless, more work, with more rigorous controls, is needed. Whatever the respective rôles of genotype and environment, these observations have an obvious methodological significance. It had been intended that the laboratory-bred wild rats should be used for experiments on social behavior; but this proved to be impossible, owing to their failure to behave in a normal way.

5.5 *Rattus rattus*

5.5.1 Social Behavior

The detailed knowledge we have of *Rattus norvegicus* is not matched for any of its congeners; but something is known of the social behavior of the other world-wide species, *R. rattus*. Ewer [229] has observed their unconfined social behavior in a man-made biotope in Ghana. Like Telle [669], she describes well-marked territories; these are smaller than the home range. Intruders are attacked or at least threatened—males by resident adults of both sexes, females only by other females. The most effective defender is the dominant male. Relationships are, however, not uniformly orderly. Male intruders usually withdraw when threatened, but not in the presence of a female in, or coming into, estrus. Clashes may then occur, and may last up to thirty minutes; but they cease when mating begins. Ewer observed one instance in which, atypically, an intruding male defeated the dominant resident male and became the dominus in his place. Even a strange female can become a member of an established group, but only with difficulty: usually, females are driven off; but they may succeed if they are exceptionally persistent.

Within a group, female *R. rattus* are evidently more belligerent than female *norvegicus*. They threaten other group members, and chase them away from food. Telle, in Germany, reports similar observations [669]. Ewer observed no formal status system among females; but she reports a linear order among the top males, though not among the younger ones. Males not only threaten other males (especially smaller ones), but also females.

Females are less discriminating than males in the objects of their attacks. They are evidently undeterred by larger size; they also play the major part in driving young adults away from the group, or at least to its periphery. Only the very young (up to perhaps about six weeks) are not attacked at all.

There is also some information on *R. rattus* trapped and observed in Scotland. Barnett [37] put members of this species in the conditions in which he had studied *R. norvegicus*. He observed the same major behavior patterns, such as crawling under, tooth-chattering, the arched-back threat posture, and the leap and bite. Among his rats, attack was, as among *norvegicus*, a male prerogative. Attack was more often opened without preliminaries, by leaping and biting, among *rattus* than among *norvegicus*. Boxing often occurred in the intervals between more violent episodes. Clashes were always between two individuals only, but a newcomer might be attacked by two or more resident males in succession. In contrast with *norvegicus*, during a violent clash the excitement sometimes irradiated among other members of the colony, which ran and jumped about wildly. Attack could not be predicted with as much certainty as for *norvegicus*. Barnett observed no evidence of differences of social rank in stable colonies. The apparent contradictions between his findings and those of Ewer may be due either to genetical differences between widely separated populations, or to the different conditions in which the two studies were made.

5.5.2 The Two Species Together

The replacement, in Europe, of *R. rattus* by *R. norvegicus* as the principal rat is a fact of history [67]. It is, perhaps, sometimes assumed that the arrival of a new species, such as the "Norway" rat, must inevitably lead to conflict with any similar species already in occupation (figure 47). Yet there are large regions in which several rodent species share a biotope, and even burrow systems, and evidently eat the same food, in apparent equilibrium. Moreover, in the laboratory at least, conflict between *rattus* and *norvegicus* is not inevitable: probably the odor of members of one species differs from that of the other, but this in itself does not provoke attack. If adult males of both species are introduced, all at the same time, into a large cage, they may live peacefully together for an indefinite period: they even huddle together during sleep [37]. Nevertheless, outside the laboratory these two species are evidently incompatible. The nearest they achieve to sympatry is the occupation of the upper floors of large buildings by *rattus*, and the lower floors and basements by *norvegicus* [704].

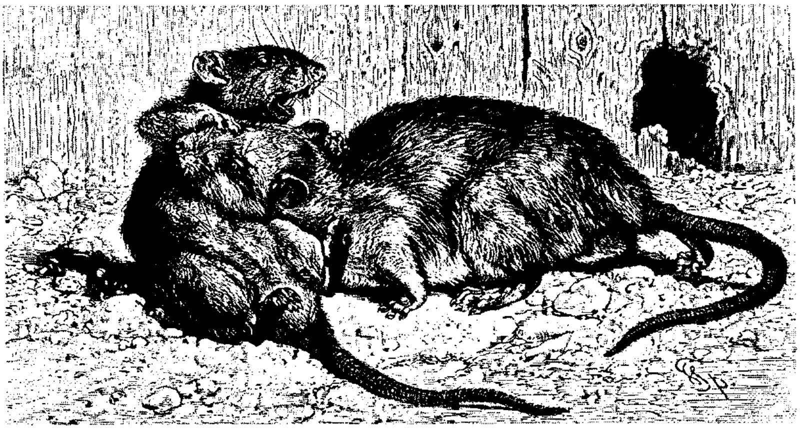


Figure 47. Interspecific conflict (an imaginary scene). The artist shows, in this dramatic drawing, a male *Rattus norvegicus* (right) seizing and biting a male *R. rattus*. Despite its apparent improbability, events of this sort have been observed and filmed in the laboratory (plate 19). (From Vogt & Specht, *Die Saügetiere*, 1883.)

In experiments, encounters between these rats resemble social interactions [37]. *R. rattus* males usually attack *norvegicus* adults which enter their territory; similarly, *norvegicus* males attack *rattus* of both sexes. These attacks occur even though a member of one species may also perform 'amicable' acts towards a resident (figure 35). As in social (intraspecific) relations, it is a territorial situation that leads to a clash: one male must be an established resident, and must be faced with a stranger. The stranger may be of either sex if it is not of the same species. Perhaps a distinctive female odor, which inhibits attack, is different in the two species: that is, while postures are shared by both species, the signs on which sexual recognition depends differ. This is to be expected. It would be disadvantageous if sexual energy were directed toward infertile union with members of another species. But the barrier of odor is imperfect. Male *norvegicus*, in their own territory, do not merely attack male *rattus*: they sometimes mix assaults with attempts at coitus. This has not been observed with female *rattus*. Perhaps the male *rattus* odor resembles that of female *norvegicus*.

The two preceding paragraphs are based on observations made in large cages in the laboratory. There are no reliable accounts of meetings between the species in natural conditions, but one was contrived in some converted stables in the south of England. A group of twenty-nine *norvegicus* and another of nineteen *rattus* were established in adjoining spaces. After two weeks the rats were fasted and a barrier between them was removed. A single food point was provided at the boundary, and the rats were watched while feeding. Members of both groups soon entered the areas newly accessible to them; whenever they intruded in a resident's nest there was much disturbance, and usually the interloper withdrew. None of the *rattus* weighed more than 200 g. A crucial event was the entry of a *norvegicus* male of 440 g into the *rattus* nests: this led to uproar which culminated in flight by the *rattus*; in this case, residence was no advantage. The experiment ended nine days after the two groups had been allowed to mix. Three *norvegicus* had died during the whole period of twenty-three days, but thirteen or fourteen *rattus* died during the last nine days. The cause of death was not established, but the asymmetrical relationship between the two species was clearly shown. The authors suggest that the superior weight of the *norvegicus* was an important factor [60]. Much more work is, however, needed on the interactions between the species. The same applies to the apparently similar incompatibility of *R. norvegicus* and *Bandicota bengalensis* mentioned in §1.1.

5.6 Co-operation and Conflict

5.6.1 Signals

Many of the general principles which govern the forms of animal communication have been illustrated in this chapter. Communication between animals depends on signals. A signal is a small amount of energy or matter which brings about a large change in the distribution of energy or matter in a system. The signals we are concerned with usually act at a distance: the source of the signal and the system influenced are both animals; the signals are *social signals* and they constitute a class of stimuli. They may (i) encourage approach and the performance of some co-operative act, such as mating or the care of young, (ii) merely prevent attack, or (iii) induce withdrawal.

Animal communication depends for its efficiency on a high degree of standardization and the use of only a few signals. This might be expected to lead to easy understanding by a human observer, but it does not do so. Our comprehension of fellow-members of our own community depends on very many indications, some given and received unconsciously and all dependent for their effect on a gradual process of learning, especially in early life: not only speech but also posture and slight movements make a major contribution. The facial muscles of expression, with the movements of the eyes, are especially important. Rats lack not only language but also muscles of expression; this is one reason why their behavior often seems to us both inconsequential and enigmatic. Another is the lateral position of the eyes. The same applies to most other animal species.

In another contrast with man, the signaling of animals is performed, nearly always, without regard to the ability of others to receive the signals. Man has some awareness of the needs and feelings of other people: although he makes many mistakes, he often adjusts his behavior accordingly. But the sounds and other signals of other species are made, as we say "automatically": alarm calls may be uttered when there is no other animal to hear them.

Yet a further difficulty arises because communication is rarely by discrete units. Although, for convenience, the preceding account has been mostly of single items of communication, such as a pheromone, posture or sound, actual signals are, as we know, often more complex: one posture may merge into another; a whistle may become a scream; and so on. Moreover, in most social situations a mammal probably responds to a pattern of information received by several senses at one time. The analysis of such patterns and the way in which they act has hardly begun.

5.6.2 Crowding and "Aggression"

Despite these difficulties, we know that the social behavior of rats, as of other vertebrates, includes both herding and dispersive interactions. Conspecifics must live for the first weeks of their lives in a family group, and must come together to mate. Ordinarily, the tendency is, even apart from family and mating behavior, to approach another rat and to associate with it in close contact. If this were the sum of the social behavior of rats, a colony would grow, as fast as its reproductive capacity and immigration allowed, until density-related factors such as food shortage prevented further increase; the rats that did survive in these conditions would remain together, many of them perhaps in an enfeebled state.

But, as we saw, social interactions probably protect most rat populations from this fate. The dispersive behavior involved is often discussed under the rubric of "aggression"—a term that in ordinary speech means "ungoverned violence" or "unprovoked assault"; yet the behavior is far from "ungoverned," and attacks are rare and are made—if at all—only under the most specific provocation. Commonly, throughout the animal kingdom, dispersive behavior consists of harmless displays ("threats") which induce withdrawal of the other [678, 679]. In human communities, an unwelcome intruder on another's ground is often regarded as an aggressor—or, at least, a transgressor; but in uncritical writings on animal behavior it is the behavior of the resident defender that is casually described as aggressive.

Despite the vagueness and contradictions of the concept, many writers invoke "aggression" as if it were some fundamental essence present in behavior generally. McNeil writes: "Theorists are in general agreement that aggression is a fundamental characteristic of existence and begins as a reflection of the action and vitality of living" [451]. There are at least three objections to this typical passage. First, there is no general agreement even that the concept of aggression is useful, let alone "a fundamental characteristic of existence"; second, the writer quoted nowhere defines the term "aggression"; third, there is no statement which corresponds to actual observations of behavior (or physiology).

The question of defining "aggression" is more than mere pedantry. The so-called "isolation-induced aggression" and "shock-induced aggression" have already been remarked (§5.4). Worse than these, in symposia on "aggression" it is common to find a gallimaufry of topics, including (i) the legal and political aspects of war, (ii) crimes against the person or against property, (iii) the physiology of the emotions, and (iv) the social behavior of animals. An extreme example of confusion is the habit of talking of "aggression" when predatory behavior is meant. Rats attack smaller mammals, birds and even fish [30, 175, 353]. This is predation: it is analogous to the behavior of cats toward mice or hawks toward chickens; its function is food-getting, not social interaction; its outcome is commonly the death of the victim. The motor patterns of catching prey of at least some species differ sharply from the postures adopted in social interactions [213]; even the neural systems involved may be separate [349].

Use of a term such as "aggression" for many diverse activities can have an unfortunate effect on the user: it may lead him to imply, and even to believe, that there is a single phenomenon to match it. "Aggression" may then be treated as something which acts on an animal, or is acted on by something in the animal. Consequently, in some writings we have the concept of an "aggressive drive": animals (and men) are said to have an inherent tendency to attack conspecifics without provocation; the "drive" is believed to build up if there is lack of the opportunity to express it. This notion, unlike many in this field, is sufficiently precise to be tested. There is no evidence for it in the behavior of rats: on the contrary, the tendency to attack probably increases with practice [53]. As might be expected on general grounds, the same applies to other species [594]. Intolerant behavior has no homeostatic function. The tendency to eat or drink increases with deprivation, but dispersive behavior is biologically appropriate only when a particular kind of conspecific is present. If an adult male wild rat is long deprived of encounters with strange males, it does not turn on members of its own group and drive them away.

Accordingly, in this book the word "aggression" is not used, except in quoting the work of others. If an animal jumps at, and bites, a conspecific, it is described as doing just that; if it postures (threatens), then it is described as doing so. In this way an attempt has been made to give unambiguous information, and to describe situations which can be recognized by any observer. At the same time physiological analysis is made easier: clearly defined movements or sequences of behavior can be related to equally distinct internal processes.

5.6.3 "Social Stress"

We now turn to some effects of intolerant behavior. Although intraspecific intolerance among rats probably influences population density, even a high degree of crowding does not, in itself, ensure conflict (§5.3.2). It is not crowding which leads to threat or attack, but encounters between adult males, strange to each other, of which one is in a familiar place. In the typical case, in nature, such an encounter presumably ends with the withdrawal of the intruder; but we have no detailed account of a completely unconfined population. Nevertheless, we know that social intolerance, both in natural conditions and in the laboratory, may have effects which are not merely dispersive. Despite the apparent harmlessness of even energetic assaults, a victim of attack, though wholly unwounded, may succumb and die without any obvious cause of death at autopsy [40, 51, 227].

To say that such deaths are due to "social stress" does not add to our knowledge. It does, however, suggest an approach to a physiological analysis [43, 46, 329–30]. There is a rather heterogeneous group of unfavorable conditions, including cold, infection, poisoning, burns and forced exercise, which induce a syndrome of responses in the mammalian body among which are increased activity of the sympathetic nervous system and increased secretion of hormones by the adrenal medulla and cortex. If exposure is prolonged, the adrenal glands enlarge (figure 48). The adjustments of endocrine function are assumed to contribute to survival, though this has not been fully demonstrated. If the animal survives, it usually becomes more resistant than before. Social interactions, too, can evoke such changes, but in this case there is no evidence that the changes are adaptive; they have, indeed, been regarded as an index of the adverse effects of social intolerance in natural conditions. We have here an anomaly which needs to be resolved. Some mammalian populations seem to display increases in adrenal cortical secretion, or at least in adrenal weight, in proportion to density [160], but others do not. Even the wild house mouse, in a field study of an island population, has failed to show this relationship. The mice initially had a density of about 740/ha, and declined to extinction for no evident reason; there was a marked failure to breed [414]. Other species which have proved not to conform with the adrenal hypothesis include the European rabbit, *Oryctolagus cuniculus* [493], the rice rat, *Oryzomys palustris* [497], and the white-footed mouse, *Peromyscus leucopus* [573].

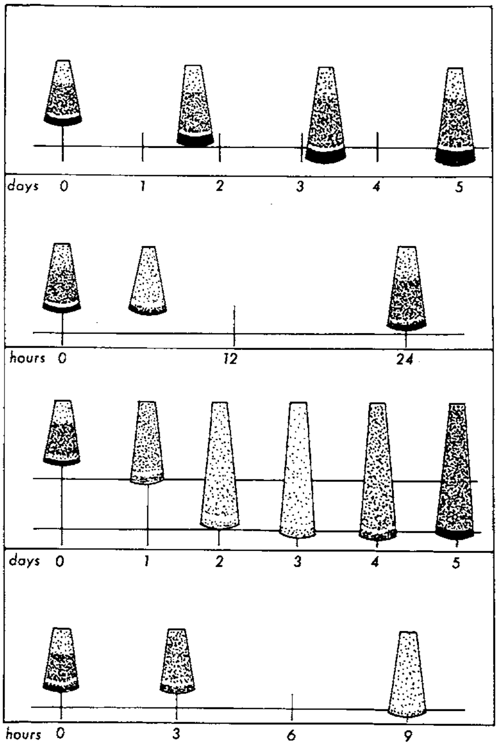


Figure 48. Diagrams illustrating adrenal responses to stressors. Each section shows a portion of adrenal cortex, with its three zones, the outer glomerulosa, the fasciculata and the inner reticularis. The appearance is that after a fat soluble stain, such as sudan black, has been used to show the cholesterol (a hormone precursor). (a) Hypertrophy due to gradual environmental change. (b) Depletion and recovery after sudden, brief exposure to a stressor. (c) The effect of more severe conditions. (d) Failure to recover. (After Sayers & Sayers [577].)

The classical account of the mammalian response to emergency emphasizes increased sympathetic activity and adrenalin secretion. The last word in the title of H. G. Cannon's famous work, *Bodily Changes in Pain, Hunger, Fear and Rage*, reflects the notion that *social* encounters can lead to an autonomic response, as well as situations that more obviously demand fight or flight. Much of the relevant recent work has been on laboratory mice [22, 155, 555, 709]. The rate of release of the adrenal catechol amines (adrenalin and noradrenalin) and also those of the brain (notably dopamine) is raised by the intolerant behavior of conspecifics; a probable consequence is enhanced responsiveness to stimulation in general. Crowded mice in the laboratory tend to have heavier adrenals, and larger amounts of adrenalin and noradrenalin in them, than uncrowded mice. Moreover, mice which frequently attack others (that is, those said to be dominant) have lighter adrenals than subordinates which are the objects of attack. Laboratory rats have been little used in this type of research, no doubt because of their marked social tolerance; but Randrup & Munkvad have described how an increase in catechol amines, especially dopamine, in the brain can provoke antagonistic behavior, such as "boxing" (shown in figure 39), among albino rats. This behavior is evidently non-specific; it is part of a general increase in activity: other features include rushing around the cage and biting at the wire walls [535].

The catechol amines of wild rats have not yet been studied, but there is indirect evidence of the expected sympathetic-adrenal activity in the laboratory: rats exposed to attack rapidly lose glycogen from their livers, but maintain or increase the level of blood glucose [51]. There are accompanying changes in the adrenal cortex: under severe attack, the adrenal cortex becomes depleted of hormone precursor; under chronic attack of low intensity, the adrenals enlarge [40]. In this species, there is evidence of adrenal hypertrophy both in animals subjected to attack and also in the attackers; hence adrenal activity is not an index of social status.

There is, as yet, no satisfactory explanation of these endocrine changes, in terms either of their survival value or of the mechanism which brings them about. There is, however, good evidence that they are not a peculiarity of *Rattus norvegicus*. Holst has made a remarkable study of tree shrews, *Tupaia belangeri*. Males were trapped, and kept isolated in cages for three months. Encounters were then staged between a resident male and an intruder. The resident attacked and "subjugated" the newcomer. The victims in such experiments lost weight; had lower liver glycogen but normal blood sugar; developed greatly enlarged adrenals; and, if exposed for long, died. All these findings parallel those on wild rats. In addition, Holst describes severe pathological changes in the kidneys, perhaps due to the excessive output of adrenal cortical hormones [329–31]. Similar changes have been observed in *Rattus villosissimus* in a state of collapse induced by social intolerance [54]. Henry and others, in a long series of experiments, have found interstitial nephritis and other kidney pathology in laboratory mice exposed to adverse social stimulation. These workers have also observed arteriosclerosis in their experimental animals [315–16]. (For this type of work, laboratory mice are much superior to laboratory rats.)

Evidently, the syndrome of changes of "social stress" involves many organs. Moreover, there is beginning to be evidence of similar changes outside the laboratory. Kidney pathology has been described by Christian and others in woodchucks, *Marmota monax* [155], and by Andrews and others in *R. norvegicus* [19], both from natural populations. The significance of these histopathological features in the growth or decline of populations has still to be discovered.

5.7 CONCLUSIONS

Social interactions may be syncretic or disruptive. In either case they involve social signals and the responses to them. A social signal may either evoke or inhibit a stereotyped behavior pattern in a conspecific.

Conflict within a group is often seemingly limited by the formation of a status system. There is no good evidence of such systems among "Norway" rats; but relationships of dominance and subordination do occur, at least among the males of experimental colonies: the viable types of male are the alphas, which are dominant but of which there may be several in a colony, and the betas, which have adapted themselves to a subordinate rôle. One alpha is equivalent to another, and one beta to another beta, as far as observation goes. Perhaps this is a primitive type of social organization, and status systems have evolved independently from it, on many lines of descent. Crowding itself does not lead to conflict: social stability depends on an equilibrium between herding and dispersal. Where there is conflict, it is possible for a rat to go short of food, even though there is plenty within its home range.

The differences between an alpha and a beta are a result of individual experience. But most of the social behavior of rats consists of stereotyped postures, sounds and odors which are probably produced without practice. The motor patterns of the two species, *Rattus norvegicus* and *R. rattus*, are closely similar, but it is possible to infer important differences in the signals (presumably odors) which evoke coitus: males of one species do not attempt coitus with females of the other. Hence a barrier between the species exists at exactly the point at which it is to be expected.

6 Reproductive Behavior

One generation passeth away, and another generation cometh.

Ecclesiastes

6.1 MATING

6.1.1 Description

Among complex land animals, an elaborate courtship is usual [68]; but rats and other small mammals are exceptions. Nevertheless, there is a large literature on the mating behavior of rats, surveyed by Beach [74–5], Bolles [100], Hinde [326] and Larsson [388]. When references are not given below, they should be sought in these reviews.

If an adult male, recently deprived of female company, encounters a female, he approaches and sniffs her; he may sniff and lick her genitalia (figure 49), or he may omit this formality and try to mount her. If the female is not in estrus, she does not allow intromission: typically she kicks the male off (plate 20), but she may merely walk away. If the female is in estrus she may herself take the initiative in approaching the male and nosing him (figure 50). After the first contact she runs a short distance (if space allows), and pauses; the male follows and mounts her; as the male presses on the female's flanks, she adopts a posture (lordosis) which permits intromission, with the coccygeal region raised and the tail to one side (figure 51). The male performs pelvic thrusts and, if ejaculation does not occur, then leaps backwards. The whole contact takes only a few seconds. After the backward leap the male sits on his haunches and licks his penis. If ejaculation occurs, the male does not leap back, but pauses and then usually falls off to one side of the female [298].

In a typical encounter, about five initial intromissions occur at short intervals without ejaculation; on the sixth, the female is inseminated; and there is then a refractory period of a few minutes, after which the sequence is repeated, but with fewer preliminary intromissions before ejaculation. The refractory periods lengthen, but ejaculations occur progressively earlier once intromissions have been resumed. There is consequently an apparent anomaly: as the readiness to copulate declines, the readiness to ejaculate increases.

This behavior is characteristic of the whole species *Rattus norvegicus*: it has been observed in various laboratory strains and much of it also among wild rats. It differs substantially from the mating of some other rodents: the male guinea pig (*Cavia*) may rest for more than one hour after a single ejaculation [733–34]. Whatever the species, the whole sequence is highly stereotyped: the typical behavior of each sex provides a clear example of a fixed action pattern.

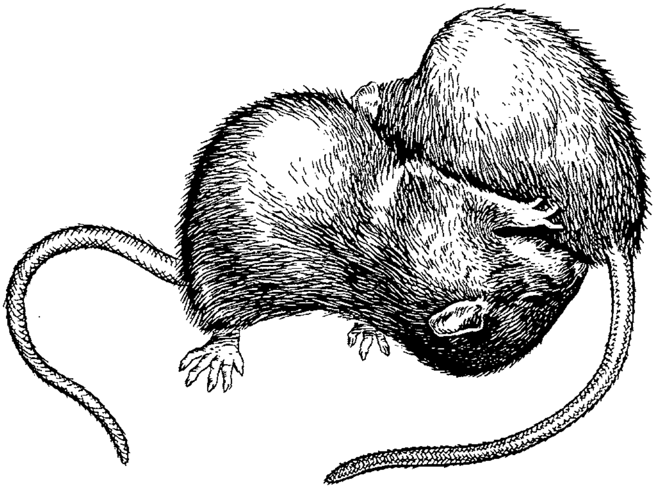


Figure 49. Mating. A male (*left*) investigates the external genitals of a female shortly to come into estrus.

The last sentence, however, does not signify that sexual behavior is invariable, but only that there is a recognizable species-characteristic performance. There is no full account of the scale and sources of variation in the mating behavior even of laboratory rats. For example, some workers have stated that ten, not six, intromissions are needed, on the average, before the first ejaculation occurs. A more extreme source of variation is social isolation: a male laboratory rat, caged alone for some time, may display markedly aberrant sexual behavior on exposure to a receptive female; recovery occurs, but only after many days [257].

There is also variation in the details of female performance. Kuehn & Beach found a receptive period of about nineteen hours, but refer to other workers who give a shorter figure. When the animals are kept on a twelve-hour light-dark cycle, the onset of the receptive period is usually about the beginning of darkness. The readiness of a female to repeat coitus depends on the behavior of the male: merely mounting is only slightly satiating; ejaculation has the greatest effect [384].

6.1.2 Signals

As we know, olfactory stimuli are of primary importance in the social behavior of rats, as of other mammals. In experiments by Le Magnen, male white rats were found to distinguish the odor of a female in estrus from that of other rats [402]. In more detailed studies, referred to in § 5.2.3, Carr and his colleagues offered male rats a choice between the odor of a non-receptive female and that of a female in estrus. Males which had already experienced coitus preferred the latter; but inexperienced males, and experienced but castrated males, did not discriminate between them [143].

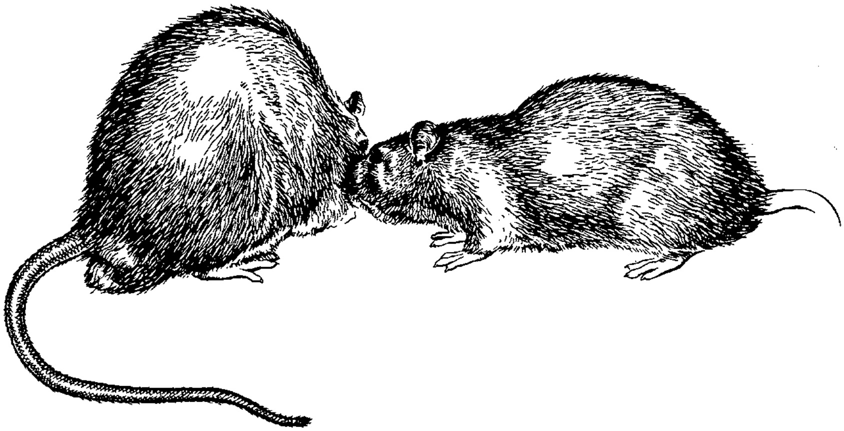


Figure 50. Mating. A female in estrus (*right*) approaches a male.

Figure 51. Coitus. The raised coccyx and deflected tail of the female make intromission possible. The pressure of the male's forelimbs on the flank is one of the stimuli needed for the female's response.

In one terminology, the odor of a receptive female would be called a social releaser. In the animal kingdom generally, social responses seem commonly to depend on single, clearly defined stimuli which often act on only one sensory modality. Among mammals, several senses seem usually to be involved, and no one is essential. This is illustrated by findings on male rats whose olfactory bulbs had been destroyed. Anosmic male rats studied by Beach did not copulate as readily as normal males, but the olfactory stimuli presented by a receptive female were not a *necessary* condition of male sexual behavior [74]. These observations have been extended by Larsson [389–90], in experiments on effects of injury to various parts of the cerebral cortex; and they have been confirmed by Bermant & Taylor. The latter compared virgin males with others that had had brief experience of coitus. (All the males had been kept in isolation for some time before the experiment, and this no doubt had some effect on the precise character of the findings.) Compared with controls which had received only a sham operation, the virgin males which had been rendered anosmic were notably slow off the mark in achieving intromission, and also took a long time to achieve ejaculation. The group which had had some experience were merely slow to reach ejaculation. Clearly, as these authors state, the effects of olfactory bulb lesions can be understood only in the light of the history of the animals studied [91].

To what stimuli does a copulating anosmic male respond? Beach studied both vision and the cutaneous sensitivity of the snout and legs. In a few experiments, two of the three senses he studied were destroyed: for instance, olfaction and vision. An inexperienced rat treated in this way failed to respond to a female, but experienced rats still copulated, evidently on the basis of the remaining sensory modalities. There was, however, much individual variation in the results of the operations. The effects on behavior of the three kinds of stimulation were evidently additive [74].

Whatever the rôle of olfaction, once a male has mounted a female cutaneous stimuli must become important. If a local anesthetic is applied to the penis, mounting is unaffected, but intromission fails or is delayed [10, 141]. Further research will no doubt make possible a more detailed analysis of copulatory behavior into components, each influenced by the input through at least three external senses.

The same principles apply to the analysis of female behavior. Females, too, are highly sensitive to male odors: whether sexually experienced or not, they prefer the odor of a normal male to that of a castrate; but this discrimination is made only during the receptive period [576]. In natural conditions, presumably a female in estrus tends to approach adult males on the basis of the olfactory stimuli they present. Once the male has mounted, the cutaneous stimulation of the flanks induces lordosis (figure 51); this can be readily imitated by an experimenter, and constitutes a useful test of the state of the female. An obvious question is whether the many intromissions which take place without ejaculation have any effect on the female. Adler studied females which had been inseminated after only few intromissions. Insemination was arranged by giving the males preliminary access to other receptive females, which were entered but not inseminated. The experimental females were compared with controls which had been allowed to mate normally. The under-stimulated females were found less likely to become pregnant and correspondingly less likely to become non-receptive. Hence multiple intromissions are evidently needed for the endocrine changes required for the normal implantation of embryos. Adler also found intromissions to contribute to the transport of semen from the vagina into the uterus [9].

6.1.3 Internal Processes

The sexual behavior of mammals depends on hormones secreted by the gonads, and the activity of the gonads depends on the secretions of the pituitary gland. Castration of a male either reduces or abolishes sexual behavior, whether the operation is performed when the rat is one day old or when it is adult. But in the second case the effect may develop only gradually: at first, behavior may be unchanged. Injection of substances chemically similar to the androgenic hormones of the testes restores sexual behavior (figure 52). The substance usually employed is a salt (the propionate) of testosterone, which is one of the steroid hormones present in testes. The same substance, given to males aged twenty-nine days, induces precocious sexual behavior; normally, sexual behavior occurs only at thirty-five days or later. It also tends to increase "spontaneous running activity" in a wheel [623].

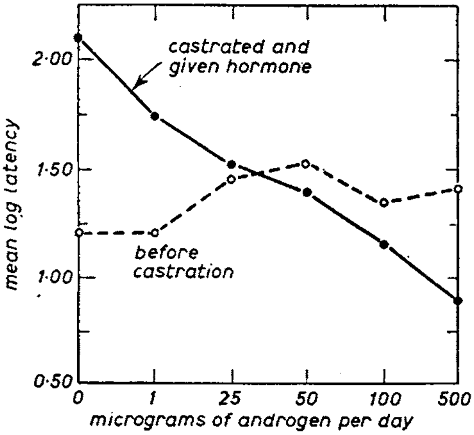


Figure 52. Hormones and behavior. The behavior recorded was the length of time (latency) before first coitus, after introduction of a female to a male. The broken line indicates the latency of control males; the continuous line refers to castrated males given different doses of male hormone. Latency declined with increasing doses. (After Beach & Holz-Tucker [77].)

The precise rôle of steroid hormones in altering behavior is not clear. The Soulairacs have described the effects of three substances on the central nervous system and the behavior of male rats. They confirm the absence of correlation between number of intromissions and number of ejaculations, in a well-controlled experimental situation in which the males were each exposed for sixty minutes to a "standard" female made receptive by a dose of an estrogenic substance (estradiol). The three substances, testosterone propionate, deoxycorticosterone acetate and diethylstilboestrol, all have a similar, excitatory effect at high doses. In this they resemble more familiar stimulants such as caffeine and strychnine. At these doses the effect was often to *diminish* sexual activity. At low doses testosterone had the specific effect of increasing sexual responsiveness already mentioned. Diethylstilboestrol at low doses tended to increase the number of intromissions, but to prevent ejaculation. It is sometimes stated that steroid hormones take effect through their general stimulating properties; this work suggests that such an indiscriminate effect occurs only at high dosages [633].

Hormones secreted by the ovaries have a parallel effect on the female. Figures 13, 53 and 54 illustrate changes in behavior which accompany changes in the amount of estrogen in the blood. When a female is in estrus, that is, receptive to a male, she is also, in certain conditions, more "active"; the figures show how running in a wheel (discussed in § 3.2.1.1) may be used as an indicator of estrus. The peak of activity at estrus is an example of the generally excitatory effect which estrogenic substances seem to exert.

If a young female is spayed, normal sexual behavior does not develop; spaying a mature female is followed by permanent anestrus and invariable rejection of the male. Responsiveness is restored if both estrogen and progesterone are injected in balanced doses. Implantation of estradiol in the region of the hypothalamus can have a similar effect (figure 54).

Endocrine effects are peripheral to the most difficult problems, those of the nervous control of behavior. We saw in § 2.3.3 how injuries to the cerebral cortex can interfere with the sexual behavior of both males and females. We cannot at present make any strong link between these crude experiments and our knowledge of the action of hormones. There are, however, five questions which can be conveniently discussed here concerning the physiology of mating and the effects of hormones on the central nervous system.

(i) The facts summarized above suggest that the central nervous organization of mating is always present in an adult, but is ineffective unless it is set going by steroid hormones. As we have seen, these hormones can increase general excitability: they evidently lower all the thresholds which bar the entrance of sensory inputs to the executive departments of the CNS. Not only is a female rat in estrus more active than at other times, but also a male, given testosterone, is more liable to threaten or attack other males and more responsive sexually.

There is the beginning of a rather more detailed analysis of endocrine and central nervous function, but it concerns the hypothalamus. Bilateral damage to the ventro-medial hypothalamus of a female rat stops the cycle of wheel-running illustrated in figure 13, and the activity is not restored by estrogen, or by other treatments which might be expected to have this effect, such as fasting or the administration of amphetamine [576]. In contrast, lesions in the anterior hypothalamus of ovariectomized rats, which also have an inhibiting effect on sexual behavior, do not reliably prevent the arousal of running activity or mating behavior by estrogen or by underfeeding. Kennedy suggests that the ventro-medial region is not directly influenced by estrogens, but has a general facilitatory effect on several stereotyped activities; the anterior hypothalamus is held to have a more specific action and to be especially sensitive to estrogenic substances [363]. Barraclough & Cross have examined another aspect of hypothalamic function. They used microelectrodes to record the activity of single neurons. They recorded the neuronal response to stimulation by cold, probing the cervix, odors, light and noise. The last two had little effect on the neurons that they studied. Their most notable finding was a fluctuation in responsiveness with the estrus cycle; in particular, odors produced the greatest effect when the rats were in pro-estrus [66]. Experiments of this kind are only in their earliest stages. They promise eventually an account in which neural function, endocrine action and behavior are firmly linked.

(ii) The experiments just described concern the motor side of the nervous system. Is this always the stage which is affected by activating hormones? Some work has emphasized the sensory side. According to Le Magnen, not only can male rats distinguish the odor of females in estrus, but they lose this ability after castration; furthermore, the ability is said to be restored by administration of testosterone [403–4]. There have been contrary findings [142], but Carr and his colleagues have confirmed the effect of sex hormones on responses to odors [143].

(iii) A third question, reviewed by Lehrman [400], is whether the effects of sex hormones are always central. The *development* of the secondary organs of sex of mammals depends on the hormones secreted by the gonads, but sexual behavior can take place without most of these organs: male rats mate normally without seminal vesicles, coagulating glands or prostate.

But this is not the whole story. Among the secondary sex characters of the rat are the papillae of the skin of the penis; these too develop only if there is enough androgenic hormone in the blood. Beach & Levinson find that the extent to which these papillae are developed influences the amount of mating behavior performed by males which have been castrated and then given male hormone. Hence the intensity of sexual behavior depends in part on this peripheral effect; the papillae are, of course, sense organs, and behavior is influenced by them through the nervous system [80].

(iv) There is next the question of the relationship between hormone action and the effects of previous experience. So far, the discussion has been in terms mainly of stereotyped activities being switched on and off; this may seem to imply that the neural organization responsible is itself fixed. But the brain is an organ of which one major function is to change performance according to individual experience. Some examples from sexual behavior have already been given. A particularly clear illustration comes from the behavior of cats. Rosenblatt & Aronson castrated male cats. The effects depended in part on the subjects' previous experience: a virgin was likely to be sexually unresponsive after operation, but an experienced animal usually displayed a persistent mating pattern. "Once organized through experience, this pattern becomes partly independent of the hormone" [557].

(v) Finally, we may consider the influence of the brain on the endocrine glands. The causal chain is far from being one-way: as must be expected, the hormones affect the brain, but the brain also influences the secretion of the hormones. The central example is the control of pituitary secretion by the brain. The pituitary cycle that controls the ovaries is itself under the influence of the hypothalamus: hypothalamic lesions alter the output of both gonadotrophic hormones. This is the physiological basis of the autonomous behavior cycle which accompanies the sequence of changes in the ovaries and uterus. The estrus cycle of a rat is typical of that of many small mammals: it is short (four to five days) and largely independent of season. It may, however, be affected by under-nutrition, and by the presence of pheromones, notably those produced by males. As we know, the behavioral changes include not only responsiveness to the male which accompanies estrus, but also much greater activity, in certain conditions, during estrus (figure 13). The nature of the "internal clock" which maintains this cycle, evidently without external prompting, is quite unknown.

6.1.4 Ontogeny

When certain behavior is said to be stereotyped, or the mating of a male rat is called an example of a fixed action pattern, it does not follow that we know how the behavior develops in the individual animal. Male laboratory rats with access to a receptive female begin mating at about thirty-five days. Mating requires maturation of the pituitary-gonad system and the consequent secretion of substantial amounts of male hormone by the testes. The behavior can be induced precociously by injecting testosterone. A question that may be asked is: If a male survives to five weeks, will it always make the typical responses to the female regardless of conditions of rearing?

This question cannot be answered. Young rats cannot be subjected to all the possible conditions which permit survival, so that we may see whether any of them interfere with the development of mating ability. We can observe only the effects of a few selected departures from the usual conditions of upbringing. The mating behavior of both sexes is then found to be notably stable in development. In the most commonly used special environment, the animal has no experience of its own species after weaning: usually, the only living beings it encounters between weaning and adulthood are the experimenters. Rats so treated respond appropriately when they meet adults of the opposite sex. Inexperienced male rats, given a choice between cavies, male rats, female rats not in estrus and female rats in estrus, rarely make mistakes.

Kagan & Beach reared over one hundred male albino rats, each alone in a cage from weaning; about half were put for ten minutes, once a week, with a sexually receptive female; fifteen were put with another male instead; the remainder had no encounters with other rats. Frequency of ejaculation, when this was tested later, was *lower* in both the groups of which the members had had regular experience of other rats. Members of these two groups had developed habits of "playful wrestling" such as occurs usually among members of a litter, and this was held to reduce the ejaculation rate [350]. It is, perhaps, not surprising that prolonged isolation, broken only by rare and brief encounters with other rats, produced atypical behavior [237, 257]. Whatever their interpretation, such observations remind us not to regard the development of fixed action patterns as simple.

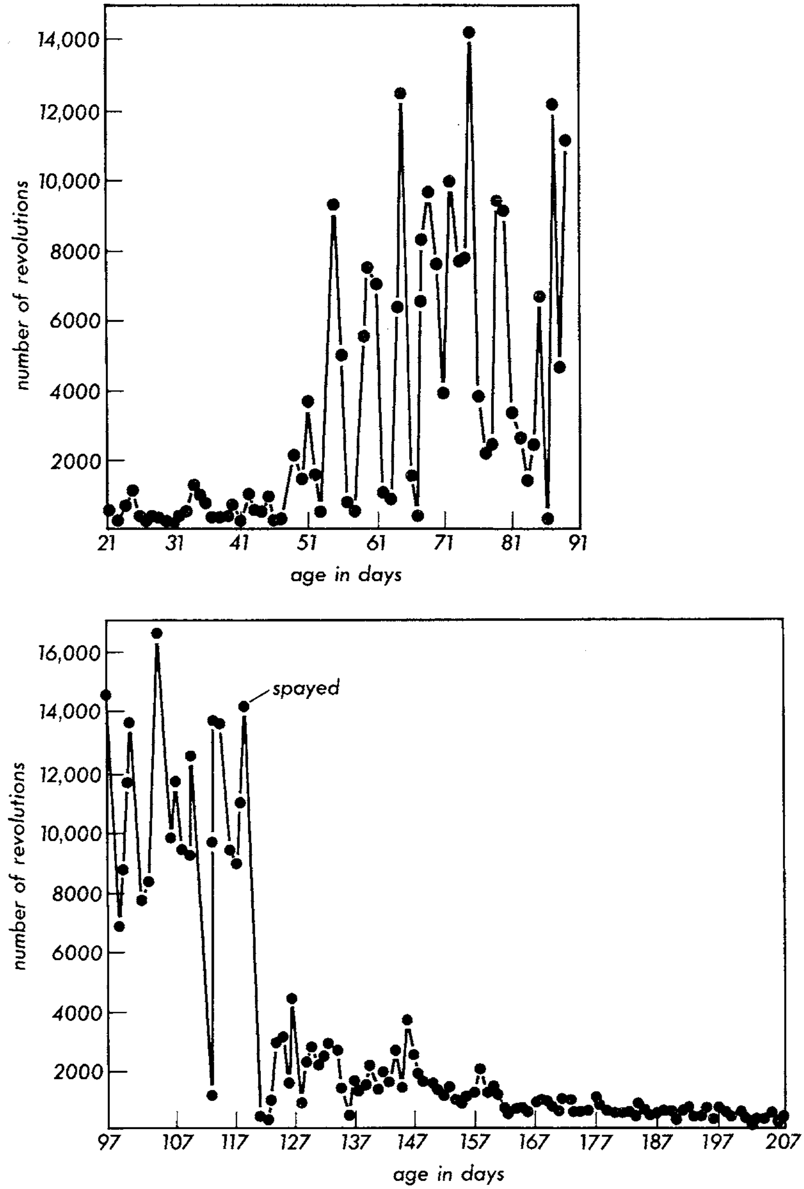


Figure 53. Hormones and behavior. (a) The four-day cycle of activity, as recorded in an exercise wheel, corresponding to the estrous cycle, begins at puberty. It is irregular at first. (After Wang [701].) (b) The four-day activity cycle ended by removal of both ovaries. (After Richter [545].)

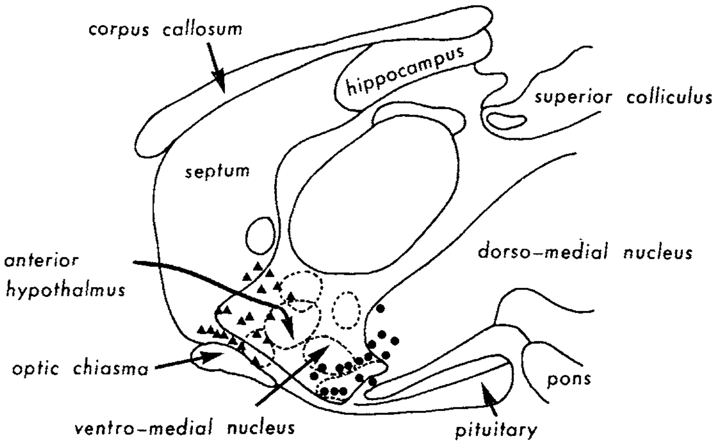


Figure 54. Diagram of sagittal section of rat diencephalon. Triangles indicate sites where implanted estradiol induces a lordosis response (see text) by spayed females. Circles show where estradiol causes increase in weight of reproductive tract. (After Sawyer [576].)

Nevertheless, these facts, with the evidence from the effects of castration, give an impression that the mating of rats is rather mechanical. We know nothing of the effects of the nestling's experience during its first few days of life; but, at least after weaning, the rat can do without encounters with its own species and still remain sexually effective. In this it resembles many non-mammalian species, but among the mammals that have been studied it is unusual. Cavies (*Cavia*) studied by Valenstein and his colleagues were adversely influenced by early isolation [690]. Often, while previous experience is not needed for the *arousal* of sexual responses, their effective *organization* depends to a substantial extent on a kind of habit formation. As W. C. Young has shown, early experience, not only of the cavy, but also of the dog, cat and chimpanzee (*Pan*), plays an important part in the development of mating behavior [733], much as it does in man. Perhaps, in this regard, the behavior of rats represents an early, that is, primitive stage in the evolution of the mammals.

Although abnormal living conditions have usually failed to throw sexual development off its course, hormonal treatment early in life can permanently change sexual behavior. The work of G. W. Harris [292–94] has revealed a sensitive period in the development of rats shortly after birth. If males are castrated at birth, their behavior as adults resembles that of a female; there is even an estrous cycle. Evidently, the development of normal male behavior depends on the hormones secreted by the testes, which act on the brain. The spinal reflexes of coitus, too, may depend on male hormone. This effect is confined to only a brief period after birth: it is evident in males castrated at the age of four days, but not in those castrated at ten days. Male hormone also influences the development of the penis: a castrate has a small penis, and this, too, no doubt, interferes with normal sexual behavior.

Females can be induced to behave like males, not by removal of the ovaries but by administration of testosterone at the age of four days. No estrous cycle develops, and sexual responsiveness is absent at all ages. If, in this state, the animals now have their ovaries removed and are given testosterone again, their behavior becomes completely male.

6.2 MATERNAL BEHAVIOR

6.2.1 General

All rats reared in ordinary conditions experience maternal care; and nearly all are reared with litter-mates. The male rat plays little part in the care of young, and usually ignores them. The behavior of the female rat towards her young has been described in detail by Rosenblatt & Lehrman [558], and by Rosenblatt [556]. More general reviews have been published by Ewer [228], Lehrman [401] and Richards [543].

The first activity of the female directed toward her young occurs, as a rule, before parturition is completed: she adopts a head-between-heels position, and licks the infant as it emerges; the newborn has its membranes neatly stripped off, the umbilical cord is bitten through and the placenta eaten. The infant is also further licked, especially in the genital region. For long this licking was thought simply to be cleaning, but it is now known to be also a remarkable and special case of cutaneous stimulation influencing the development of behavior. Reyniers & Ervin tried to rear rats from birth artificially. The young accepted the milk offered in a "bottle"; but they failed to release their urine and feces in the normal way, and so died. This failure was found to be preventable by gentle stimulation of the perineal region. The reflexes involved require this stimulation before they become effective [542].

Once the post-partum operations have been carried out, the female displays further stereotyped responses: these include adopting the nursing posture, which allows the young to suck, retrieving strayed young (plate 22), more licking, nest-building and defending the nest. All these activities, with the possible exception of defense of the nest, are performed by both wild and laboratory rats. They have, however, been analyzed experimentally only in the laboratory varieties.

6.2.2 Nest-Building

Given the opportunity, any rat makes a nest, at least of a hollowed-out heap of material; the site is under cover as a rule, often in a burrow. The material—straw, fragments of cloth or sacking, paper and so on—is carried in the mouth. It may be torn up and fluffed out. Kinder gave paper to rats aged twenty days with no previous experience of nest-making: they built a nest within three hours [365]. Rats do other constructional work also. Plate 23 illustrates the filling in of spaces in the walls of wire cages with a mixture of dung and cotton wool; the screen is made with a rapid, stereotyped patting of the forefeet—a procedure which is perhaps important in the construction of earth burrows.

Several factors, apart from maternity, influence this behavior. Temperature is certainly important. Kinder's rats tore off increasing weights of paper for nest-making as the surrounding temperature was lowered [365]. Denenberg and his colleagues offered rats small wood cylinders or dowels. The dowels were shredded and the weight of wood removed in this way proved to be a good measure of nest-making activity. Both males and females substantially increased shredding when the ambient temperature was lowered from 21 °C to 13°C [195]. Screen-building, described above, occurs only at the front of a cage and on its roof; factors may be currents of air, or light. This needs investigation.

The homeostatic significance of nest-building has been more subtly displayed by Richter. He destroyed the pituitary gland and so induced degeneration of the thyroid; his experimental rats consequently had an impaired ability to increase metabolism on exposure to cold. The result was improved nest-making. Thyroidectomy had a similar effect [544]. Figure 55 shows a form of Skinner box in which depressing a panel switches on heat; rats in this apparatus learn to adapt their behavior to their need for warmth. Thermoregulatory behavior is further discussed in § 9.2.1.

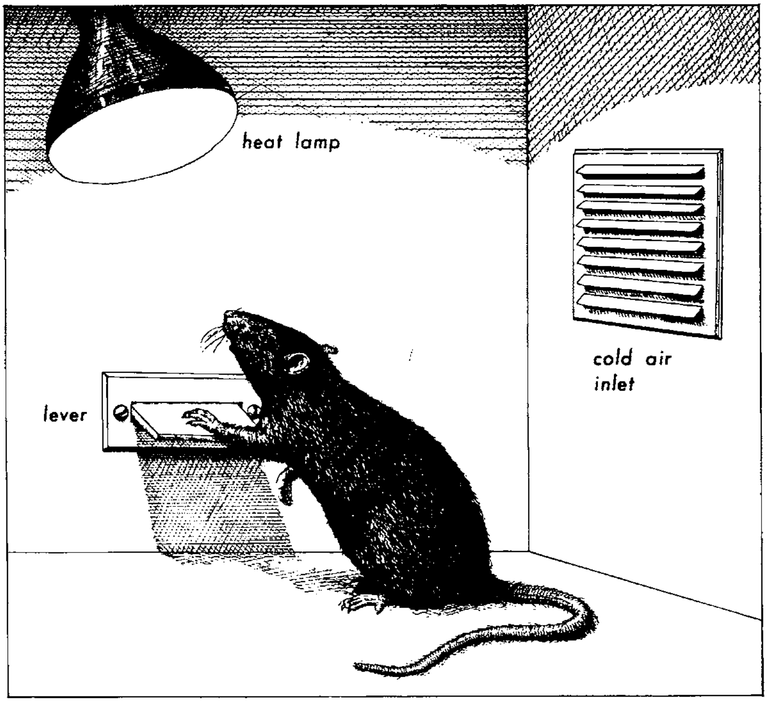


Figure 55. Skinner box in which the reward of pressing the panel is the switching on of a source of heat. Rats adjust their response rate to their need. (After B. Weiss [707].)

The nest-building of maternal rats by contrast is largely independent of external conditions. A female in late pregnancy builds a substantial nest in a wide range of temperatures. Gelineo & Gelineo gave parturient females a choice of environmental temperatures in which to build: they settled at about 16°C, much below thermal neutrality (the temperature at which resting metabolism is minimal). These authors believe that this ambient temperature favors the growth of the young [254]. At the ordinary laboratory temperature, the nest made during the three to five days before parturition is open at the top; when the litter is born, more material is added: the female first covers the litter, then shapes the structure from outside and finally forms a domed cavity within. From about ten days after parturition, the space inside the nest is enlarged, and the structure is left open, with progressively lower walls. If the nest is removed, it is made again, but not after about fourteen days from parturition. The building and maintenance of the maternal nest after parturition depend on the presence of the young. If the young are removed at birth, and the nest is destroyed a week later, many females fail to restore it.

6.2.3 Concomitant Behavior

The behavior of a pregnant or lactating female is distinctive in ways which do not directly influence her young. Although nest-building increases during pregnancy, total activity probably declines. Most studies of "activity" in pregnancy have been of behavior in a running wheel (§ 3.2.1.1). Wang recorded a marked decline in running during the period around parturition [701]. The activity of female mice, virgin, pregnant and lactating, has been studied in an artificial environment of the kind illustrated in figure 14. This arrangement has the advantage of allowing the female to get away from her litter from time to time; indeed, it obliges her to do so, just as she would in natural conditions. Figure 15 shows a decline in two aspects of "activity" in late pregnancy, and a gradual recovery during lactation. It also shows how some "unrewarded" exploration continues even at the time of the birth of a litter. Despite the decrease in activity, food consumption rises during pregnancy, and still more during lactation.

The changes in activity and food consumption accord with expectation. Other behavior has a less obvious function. All rats clean their body surfaces from an early age: the self-grooming of an adult is an elaborate, stereotyped sequence (figure 56) which has been little studied. The following notes record the behavior of a wild rat on waking:

> Eyes open. Rises and stretches. Licks hands; washes face; washes behind ears, and continues to lick hands at intervals. Licks fur of back, flanks, abdomen. Licks hind toes, scratches with them; licks, scratches . . . ; hind toes scratch flank and belly from front to back. Licks genitalia. Licks tail while held in hands. Licks hind legs held in hands. Bites fur. [47].

This sequence is typical of both wild and laboratory rats, of both sexes. The behavior seems to be performed regardless of need: the animal evidently does not wait until parasites or dirt demand attention. Little is known of the factors which influence the readiness to groom: perhaps the accumulation of skin secretions plays a part; no doubt the presence of foreign bodies on the skin stimulates grooming.

During pregnancy the self-grooming of a female changes: she increasingly licks the skin around her nipples and external genitalia. At parturition the licking is intensified, and is accompanied by licking of the young as they are born. The significance of this behavior has been tested by preventing it. Female rats were fitted with wide rubber collars, which resemble Elizabethan ruffs (figure 57), and which prevent self-grooming. The mammary glands of these females at parturition were underdeveloped and resembled the glands of normal rats only about half-way through pregnancy. Evidently self-licking stimulates mammary development [546]. Preventing self-licking during pregnancy has also been said to result in failure of maternal care, but attempts to confirm this have failed [561–2].

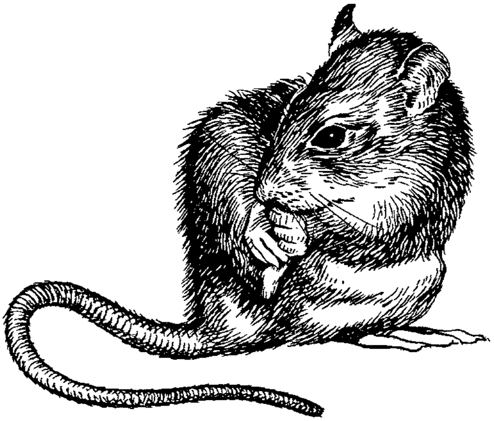


Figure 56. Grooming.

6.2.4 Care of Young

6.2.4.1 *At parturition.* The onset of parturition is marked by waves of muscular contraction, while the female lies stretched out. During delivery of the young rats, contractions continue, but the mother stands, head between legs, and uses her mouth to free the young from the membranes and to help their emergence. The amniotic fluid released when the membranes are ruptured is licked, as well as the newborn.

The placentae are eaten. This behavior is less surprising in an omnivore, such as a rat, than in some other mammalian species which—though wholly plant-eating—also become carnivorous on this one occasion. What prevents females from eating their young as well? The same problem arises in the behavior of males. As Myer has pointed out, some rats regularly attack mice, but refrain from violence against rat nestlings. Myer altered the olfactory properties of young rats, and brought evidence that it is their odor which prevents at least male rats from killing them [491]. (Occasionally the inhibition fails, and the young are slaughtered and consumed.)

Figure 57. Rat with collar to prevent self-grooming. A similar fitting can be used to prevent passage through a hole or tunnel.

6.2.4.2 *Lactation.* As a result of the enlargement of the mammary glands during pregnancy, and of other changes, easily digested food is available immediately for the newly born young. In the typical nursing posture, a rodent crouches over her litter. The readiness to take up this position is determined by a female's hormonal state; the immediate stimulus to do so is the presence of young. Pressure in the mammary glands also plays a part, though it has not been possible to study this in rats. The secretion of milk depends on the presence in the blood of hormones of the anterior pituitary, especially prolactin. The pituitary stalk of a lactating rat may be cut; the action of the hypothalamus on the pituitary is prevented, pituitary secretion declines, and the supply of milk quickly diminishes.

If the young are removed from a normal lactating female, the mammary glands soon regress and milk secretion ceases. This is partly due to a local effect of sucking: nestling rats in small litters usually suck only from the front nipples; the other glands then regress. The influence of the presence of young can also be used to prolong lactation: Wiesner & Sheard regularly removed older litters and replaced them by younger ones; female rats so exploited continued to give milk for several times their normal term [714].

The effect of sucklings is not only local. The act of sucking by infant rats stimulates the secretion of prolactin by the pituitary. This action is mediated by the sensory nerves of the mammary glands: if some nipples are denervated, stimulation of the other nipples still increases the rate of secretion of all the mammary glands. According to Grosvenor & Mena, the effect of infants on prolactin output does not depend on sucking, but can be evoked merely by exposing a lactating female to the odor, sight and sounds of the young [276].

The mammary glands are complex effector organs: they not only secrete milk, but also eject it ("let-down"). There are myoepithelial cells in the walls of the mammary alveoli, of which the contraction increases the pressure within the alveoli; the sucking infant then receives a jet of milk. This reflex, though primarily a response to the sucklings themselves, is also influenced by other social stimuli: Deis allowed lactating rats to hear, but not see, other rats with their sucklings, and so increased milk-ejection. If females so treated were deafened, there was no such effect [191]. This is a special form of social facilitation.

In the experiments by Deis, the action on the mammary glands of his experimental rats was through their motor nerve supply; the other systemic influence on the mammae, the endocrine, can act independently. If the anterior part of the hypothalamus is stimulated by means of implanted electrodes, milk-ejection follows, evidently not as a result of a neural motor output but through an effect on the secretion of a pituitary hormone which acts on the mammary glands.

6.2.4.3 *Retrieving.* The maternal behavior most studied is retrieving. The carriage of straying or fallen young back to the nest is easily observed and timed in standard conditions. Beach & Jaynes have revealed some of the signals which evoke the retrieving of young. Lactating females were watched in a standard situation. Some were presented with young whose properties had been altered, for instance by smearing them with an odorous substance. The features of the young which helped their mothers to retrieve them included visual, chemical and tactile components; temperature also had some effect. (Other evidence, such as that of Wiesner & Sheard mentioned above, had already suggested an importance of the squeaking of the young.) None of the sensory modalities was indispensable [78–9]. As with the mating behavior of a male, so with retrieving of young we find multisensory control of a stereotyped pattern.

A further feature of the young which influences retrieving is their size. The work of Wiesner & Sheard not only demonstrated this effect but also illustrated much variation between individuals in the performance even of a stereotyped act. Retrieving was studied immediately after parturition, and some females responded even to young aged as much as six weeks. Usually, the tendency to retrieve declines markedly with the growth of the young. If an old litter is removed and replaced by a younger one, the intensity of retrieving is raised, just as milk secretion is stimulated. Repeating this procedure can prolong the period of retrieving by some females to over four hundred days [714].

Something is known of the internal processes which influence the components of maternal behavior [543]. Retrieving is unaffected by destruction of the mammary glands [467]: hence it is not controlled by the engorgement of the glands with milk. The major peripheral control is that of hormones [469]. Spaying does not alter maternal behavior, but interference with pituitary secretion may do so. Hypophysectomy is usually followed by failure to behave maternally. There are, however, exceptions to this rule. Cosnier & Couturier have described maternal behavior by nulliparous females. This behavior develops only after the females have had access to young for six days or more [173]. By contrast, a parturient female responds to nestlings at once. Moltz and others have gone far to explain the confusing findings in this field by combining three hormones in experimental treatments. They spayed adult females, and injected estradiol benzoate daily for eleven days; they also gave progesterone on the sixth to ninth days and prolactin on days nine and ten. On day ten the females were each offered six newborn rats; all responded maternally within forty hours. Controls which had not received all three hormones did not [467]. Evidently, as in other processes regulated by reproductive hormones, the synergistic action of several such hormones is needed for normal function.

Maternal behavior must obviously be highly efficient if the young are to survive. Accordingly, in a quite wide range of conditions it is remarkably uniform. This does not, however, preclude variation due to differing conditions in early life; nor does it rule out the possibility that females to some extent learn to behave maternally. Experiments on these questions have revealed notable stability in the development of maternal behavior. Thoman & Arnold reared females in isolation from other rats from birth; the young rats had to be fed by hand. Despite this bizarre upbringing, the experimental subjects became satisfactory mothers [671].

Nevertheless, as Cosnier has shown, even these observations leave open the possibility of improvement with practice [172]. Moltz & Robbins studied nursing, nest-building and retrieving among albino rats in typical laboratory conditions. They detected no difference between females with their first litter and those with later litters [470]. In the same year, Carlier & Noirot reported an opposite finding. They observed female rats on seven successive days after the birth of the first litter, and the same rats for the same period after the birth of the second litter. Each female was in a cage with two compartments, in one of which the young were reared; the second compartment was used to confine the female while her young were moved out of their nest to a position from which the female could retrieve them. All litters were reduced to five young at birth. The females were familiarized with their double cage from early in their first pregnancy. During the first seven days of the first lactation there was a marked improvement in performance: in particular, the median time taken to retrieve all the young fell from above seventy seconds almost to thirty seconds. The corresponding figure at the beginning of the second lactation was below thirty seconds; hence the skill developed in the first phase was retained, and perhaps improved, during the interval before the second litter was born [139].

Interpreting these findings is not simple. It is, indeed, difficult to design rigorous experiments of this sort. Can we conclude that the superior performance with the second litter was an example of learning by practice? Unfortunately, the factor of age was not controlled: inevitably, in these experiments, each female was not only biparous in the second phase, but also older than in the first phase. Another question concerns the young: it is just possible that the members of a second litter are more effective in provoking maternal care than members of the first. To satisfy all requirements, it would be necessary to carry out more elaborate experiments than, evidently, have so far been attempted.

A final question on retrieving concerns its significance in natural conditions. Removal of the young to a standard distance from the nest makes a convenient experimental procedure, but does not mimic anything that commonly occurs in nature. Carrying young to a nest may, in normal conditions, be of greatest importance in relation to disturbance of the environment. A lactating female, in a more complex environment than a small cage, often responds to disturbance by moving her litter, one by one, to a new nest. Wild females do this on the run ([47]: plate 22). Although much is known of the factors that influence retrieving by laboratory rodents, some doubt must remain on the rôle of retrieving abilities for the various species in natural habitats.

6.2.4.4 *Maternal pheromone.* In most experiments on the interactions of mother and young, the young are treated as the passive recipients of maternal attention. This is satisfactory for some purposes, especially when the first postnatal days are considered. Nevertheless, even in their apparently helpless period, infant rats and mice not only make noises that influence the mother (§ 6.3.1), but also have some capacity to move from a cold place to a warmer one [504].

There is a later period when nestlings are mobile but still depend on the mother. They then stay with the mother through their own efforts, and retrieving by the mother declines. Leon & Moltz have given evidence of a pheromone, produced by female laboratory rats, which attracts older nestlings. They used a simple apparatus to test the ability of rats aged sixteen days to move toward the odor of a female in the sixteenth day of lactation; the alternative offered was the odor of a non-lactating female. Any lactating female will do; there is no evidence that individuals are recognized. The earliest day on which the pheromone has been detected (by the responses of young rats) is the fourteenth day of lactation; the latest, the twenty-seventh (that is, the normal time of weaning) [406–8].

Secretion of the pheromone depends on the production of prolactin by the pituitary (compare § 6.2.4.2); but it does not depend on lactation: if the secretion of milk is prevented by removing the adrenals or the ovaries, the pheromone remains. Moltz & Leon have, however, demonstrated another factor necessary for production of this substance: if a female is given only newborn young to nurse for fourteen days, she does not become attractive to mobile young at the fourteenth or later days of lactation. The presence of active young is required for secretion of the pheromone. Like other features of maternal performance, this one evidently requires both a particular internal state and specific external stimulation [468].

6.3 INFANCY

6.3.1 Features of Early Behavior

A female rat with her young displays a series of species-characteristic activities. This statement implies a high degree of uniformity in the behavior. Nevertheless, there is substantial variation in the conditions that an infant rat can survive; variation may be in maternal performance as well as other features of the environment. The rate of development of the young and many aspects of adult performance may reflect these early influences.

"Rate of development" may refer to total growth rate, but this is the resultant of many forces; and not all developmental rates go with body weight. The development of behavior is marked by the appearance of a number of "reflexes" and orientations which can be easily recorded. The newborn rat responds to a nipple or similar object by sucking; orientation to the nipple is probably aided by odor. Maternal odor has an additional effect. Schapiro & Salas studied the movements of rats aged from two to eleven days: the amount of movement, mechanically recorded, was much lower when maternal odor was present than when it was absent; hence in this case a pheromone has an inhibitory effect [579]. Infant rats are, of course, not totally inactive when the mother is present: movements which, when performed by larger mammals, are called the "milk tread" help to stimulate milk secretion and letdown. These activities seem to develop "spontaneously"; but further study might reveal that the female plays a part in evoking them. Reflexes of elimination also develop shortly after birth; these depend on the young being licked by their mother [§ 6.2.1]. A probably important motor ability is the production of sounds. Nestlings squeak and make clicking noises, especially when their stomachs are empty or when their skin temperature falls [714]. Some of the sounds are of too high frequency for human ears. Noirot describes ultrasounds of 35 to 55 kHz, which she calls distress calls. These are infrequent during the first three days, but increase with the opening of the pinnae. The maximum is between five and ten days; by sixteen days they are again few [501].

Responses which first appear rather later (reviewed by Smart & Dobbing [622]) are more useful as indices of developmental progress. Among them is the startle response to a sudden noise (Preyer reflex). During their first days infant rats have closed ear passages; possibly more important, the nervous system is undergoing rapid development. Responses to noise are not evident during the first week after birth, and a full startle response occurs only at or after the eleventh day. Later, probably around the fourteenth day, the eyes open; this, too, is an index of neural maturation, for it indicates functioning by the motor supply to the muscles which raise the upper eyelids. At about the eighteenth day the full righting response appears: the young rat, if dropped, lands on its feet (just like a cat) regardless of its initial orientation.

Progress is also marked by the ability to direct movement so that the long axis of the body is in line with a source of stimulation. These orientations are called taxes (formerly "tropisms"—now reserved for the bending of plants) [242]. Fixed orientations, which are conspicuous in the behavior of many invertebrates, are largely submerged in the more complex and variable movements of an adult mammal. Nevertheless, a young rat early develops a well-marked negative geotaxis: once it has reached a certain age, if put on a sloping surface, it tends to move upwards. A young rat also becomes thigmotactic: set to walk alongside a vertical surface, at a corner it turns so that it maintains contact with the wall.

These abilities clearly depend on the development of special sensory functions. Another kind of sensory ability is the perception of distance. Any terrestrial animal above a certain size must be able to avoid falling as soon as it becomes active; if it depends on vision, it should be able to judge distances, especially vertical ones. In 1934, Lashley & Russel required rats to jump from a stand to a platform of which the distance could be varied (figure 7). Rats reared in the dark were able to jump as accurately as control animals [395]; but the dark-reared rats needed a little experience of light before they would jump, and so the experiments were not conclusive on the character of the development of this ability.

A different type of experiment, reviewed by Walk [698], has given remarkable and detailed information on the early perception of vertical distances by several species, including kittens, goats and man. A "visual cliff" is used (figure 58): a narrow platform has plate glass flooring on each side; on one side a patterned floor is just below the glass, while on the other the floor is some distance below, giving the appearance of a cliff. Hooded laboratory rats (unlike the other mammals mentioned) show little preference for the two sides, provided they can feel the glass with their vibrissae; but if the central platform is raised a few centimeters, so that the glass cannot be felt, the rats nearly always choose the shallow side. If there is no visible pattern on either side, no preference is shown. This ability is evident among rats as soon as they can see [418] and is not prevented by a period of rearing in the dark [145]; but if the vibrissae can function, the sensory input from them is more important than vision [581].

Many other responses are distinguishable in infancy. Blanck and others give a more detailed account of "orienting behavior" [98]. The examples described above show that infant rats possess a repertoire of stereotyped behavior patterns and of sensory arrangements which (i) have obvious survival value and (ii) seem to be as fixed in development as are structural features such as the shape of the ear or tail (both used in classification) or chemical effects such as hair color. Nevertheless, although these early performances seem remarkably uniform, they do vary; and in § 6.3.2 below we turn to some of the sources of this variation.

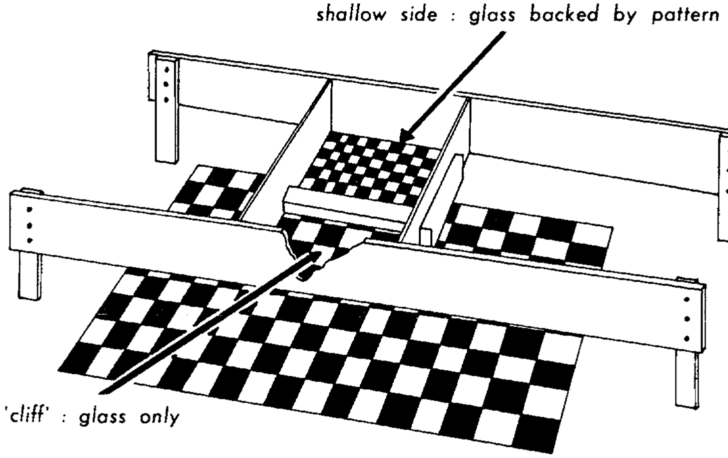


Figure 58. Diagram of visual cliff apparatus. An animal is put on the central platform. On the far side the appearance is of a shallow step down; the near side looks like a cliff. There is, in fact, a safe platform of plate glass on both sides. (After Walk [698].)

A conventional age to mark the end of infancy is twenty-one days. This is a suitable age for weaning a laboratory rat, that is, for removing it from its mother. Wild rats do better if left for about twenty-eight days [41]. Even before weaning, a number of juvenile activities become prominent. Bolles & Woods have described them for albino rats. There is a sharp increase in exploratory behavior after the fourteenth day; and "play" becomes conspicuous about the eighteenth day [102]. Between weaning and sexual maturity there is a period of some weeks which has been little studied behaviorally. It is marked, especially among wild rats, by the performance of activities which become effective only when the animals are fully adult. Among those seen are the components of attack, crawling under, and mounting as in coitus, but not, evidently, adoption of the nursing posture; objects are carried, as in nest-building. All this differs from adult behavior in two respects: (i) it is not specifically directed behavior, and (ii) it leads to no outcome. Attack is not directed to intruders; and one juvenile may attack at one moment, be attacked at the next. Coitus is not completed. No nest is built. This behavior, then, is "play": it belongs in a heterogeneous group of phenomena which still lacks experimental analysis.

6.3.2 The Early Environment and the Ontogeny of Behavior

In the experiments now to be described, the experimental animals were subjected to conditions in early life which departed from those in which laboratory mammals are usually reared. The experimental treatments, as Schaefer [578] has remarked, have often been named by terms which seem to reflect the bias of the experimenter: gentling, trauma, stress, stimulation, manipulation and so on. The present interest in the subject arose in part from remarkable observations, in which handling infant rats improved their resistance to adverse treatment, such as wounding, later in life. A sudden rush of experiments after 1950 has led to no clear picture [2, 133, 183, 500, 578].

One source of difficulty in interpreting the findings is the diversity of treatments used: they include not only handling, but also exposure to cold, mechanical shaking, loud noises, bright light and electric shock. Other variables have been the species or variety studied, and the age at which the treatment was given. Moreover, sometimes a given treatment has had opposite effects in different hands, or even in the same hands on different occasions.

W. J. Meyers subjected just-weaned rats aged twenty-one to twenty-three days to one of a series of treatments: the controls were left undisturbed; the experimental groups were (i) "gentled" by an experimenter, (ii) roughly handled, (iii) immobilized for a period—a "stressful" procedure, (iv) given mild electric shock or (v) given severe electric shock. Members of all the experimental groups except those "gentled" developed stomach lesions of a type which may become ulcers; in other words, all these four treatments were to some extent injurious. The group that received severe shock also grew less well than the others. "Gentling" and mild shock increased the readiness with which the rats later explored a novel environment: (that is, in the anthropomorphic terms often used in this context, they displayed less "emotionality" or "anxiety"). Meyers interprets these rather complex findings in the manner illustrated by the "inverted **U**" of figure 23: mild early stimulation may be regarded as having a favorable effect on development (represented by the ascending parts of the curve), while more violent treatment is unfavorable [457]. Denenberg [194] and Goldman [264] have discussed this model. It shows how even the same type of experimental treatment, at different intensities or applied to subjects of different susceptibilities, could give opposite results.

The model is, however, too simple to account for all the facts. It is also obvious that, to produce anomalous findings, the **U**-shaped curve need not be inverted. Henderson, like Meyers, exposed rats to a variety of treatments, but at an earlier age. Some of his animals were reared in the usual conditions of a laboratory, others in restricted conditions. During infancy, rats of each group were either (i) subjected to electric shocks, or (ii) regularly handled, or (iii) left undisturbed. The effects of the three treatments, especially those on the animals given a restricted early environment, yielded a **U**-shaped curve, but this time the U was the right way up. The test, applied at the age of seventy days, was the conventional one of performance in the open field. The lowest defecation rate ("emotionality") was that of the rats exposed to the moderate early stimulation of handling; both the shocked and the undisturbed groups scored higher [314, 457].

In many other experiments, laboratory mammals have been mildly "stimulated" in various ways in early life. In a long series of studies, reviewed by Rosenzweig [560], rats aged between about twenty-five and eighty days were reared in one of two environments, "enriched" and "impoverished": the former included other rats, and a variety of objects which were varied daily.

The impoverished group lived alone in featureless cages with solid walls. The findings are described in terms of the effects of an "enriched" environment; but, since the "impoverished" is by far the less natural, it is at least equally appropriate to express the results as effects of the restricted conditions. The weight of the cerebral cortex of the impoverished group was about 4 percent less than that of the enriched. This is attributed, not to neuronal differences, but to the presence of fewer glial cells. A number of chemical observations were also made, notably on the group of enzymes called cholinesterase (ChE). ChE catalyzes the breakdown of acetylcholine, the neurohumor of neuromuscular contraction and of central nervous transmission at synapses; and ChE activity was lower in the cortex of the impoverished rats.

These findings, which have led to some debate, are difficult to interpret, and have not yet been linked with the larger body of researches on the effects of early rearing on later behavior. In these studies the treatments have usually been applied before weaning.

Levine & Mullins [412] have reviewed some of this work. They are particularly concerned with the apparently favorable effects of early mild stimulation: in natural conditions, small mammals are held to lead a much more disturbed life during their first weeks than laboratory mammals in cages; from this point of view the latter should be regarded as the experimental subjects. (An opposite opinion has been put forward by Daly [183], in a critical survey.) In the experiments discussed by Levine & Mullins, laboratory rats or mice are picked up and isolated for about three minutes daily during their first three post-natal weeks. They and controls are put as adults in a novel environment (an "open field"), in which they are allowed to wander for a short period. As in the experiments by Myers and by Henderson, described above, the animals which have been disturbed in early life usually move about the open field more readily; moreover, in the usual type of experiment rats (but not mice) defecate less. Accordingly, the stimulated animals are, as we saw above, said to be less "emotional" [412]. Stimulation in infancy also accelerates certain features of development, such as the appearance of hair, the opening of the eyes, and the development of locomotor abilities.

Levine & Mullins give evidence that these effects are accompanied by changes in the response of the adult endocrine system to environmental hazards. Mild stimulation of adults, such as exposure to a novel environment, is accompanied by adrenocortical activity lower than that of controls; but, after the more severe stimulation of an electric shock, control animals have less corticosterone in the plasma than the experimentals. The role of the hormones of the adrenal cortex is not fully known; hence the significance of changes in their secretion rate is uncertain. They are secreted in larger amounts if an animal is exposed to cold, infection, burning, loss of blood and (as we saw in § 5.6.3) certain types of social stimulation. Perhaps the full development of the physiological response to "stressors" by hypothalamus, pituitary and adrenals depends on a level of early disturbance or stimulation which is not reached in the typical environment of the laboratory. This hypothesis, reviewed by Denenberg & Zarrow [198], has provoked much interesting experimental work. It has also led to controversy: Ader & Grota, for instance, review a number of conflicting findings [8]. One possible source of confusion is variation in the animals or methods used.

The importance of the precise character of the early stimulation is brought out in a review by Schaefer [578]: in certain experiments, early handling has had an effect on behavior in the open field only if the treatments were applied during the first post-natal week; treatments in the second or third weeks were ineffective. What is the crucial component of the favorable stimulation? In most experiments of this kind, the subjects are exposed to some degree of cold: the temperature even of a warm laboratory is lower than that of a nest in a cage. Of course, these experiments also require separation from the mother; but Schaefer, in some of his experiments, controlled for this by removing the female from her litter, instead of some members of the litter from her: this produced no effect on the time spent crouching motionless in an open field, although handling plus exposure to cold did so. It is, perhaps, hardly surprising that removal of the mother for brief periods left the young unaffected, since in natural conditions a female inevitably leaves her nest from time to time even when not disturbed by an experimenter (compare § 6.2.3). Much more work is, however, needed, before the exact rôle of cold can be assessed.

One source of difficulty is the interaction of the effects of early stimulation with other features of the environment. Ader has studied (a) the development of gastric erosions, and (b) the "emotional" response of rats to handling, in relation to (i) early stimulation and (ii) isolation. Some of the rats he used were derived from a strain exceptionally susceptible to gastric erosions. Erosions were induced at about four months by immobilizing the animals in wire mesh for six hours. Regular handling during the first three weeks after birth decreased the incidence of erosions, but only among the rats which had been kept in isolation [5].

A further factor is the response of the mother to interference with her young. From conception to weaning, the development of a mammal depends on a continual interaction between mother and offspring, in which each stimulates the other. Ressler has illustrated this by using two inbred strains of laboratory mice, BALB/c and C57BL/10. Litters of each strain were fostered on to parents either of their own strain or of the other strain: there were therefore four types of situation, which allowed analysis of whether the two strains differed in parental performance or in the extent to which the young provoked parental attention. The BALB mice spent longer attending to their young, regardless of the strain of the latter: at the same time, the BALB young attracted more attention from their foster parents, regardless of *their* strain [540].

The importance of the intensity of parental attention for the development of the young is suggested by observations, also on laboratory mice, by Barnett & Burn. They exposed one mouse from each litter studied, for ninety minutes a day from the sixth to the eleventh post-natal day, at 21 °C, and another at 34 °C. A third mouse had a hole punched in one ear but was left in the nest, and yet another was also left in the nest but with no hole. The experimenters handled all mice to the same extent. The result was disconcerting: the principal difference was between the control mice with no holes in their ears, and the rest; all classes of mice with holes in their ears, including the "controls" which were left in the nest, survived cold exposure at the age of twenty-two days much better than the controls with normal ears. The injured mice were also superior than the others in several indices of maturation. In a further series of experiments Barnett and Burn watched the behavior of the parents toward their young: those with holes in their ears received more attention than the others, whether they had been exposed outside the nest or not. Accordingly, the differences in maturation and cold resistance are tentatively attributed to the effects of different amounts of parental attention, that is, licking, nuzzling, biting and carrying [50]. Barnett & Walker have confirmed the effect of injury to a nestling mouse on the maternal attention it receives. They also find marked changes in the temperature of young mice accompanying the licking and other treatment administered by the mother [65]. Just how these fluctuations influence development remains to be found out.

If the effects of injury, or of exposure outside the nest, are due to changed parental behavior, these findings have considerable methodological importance. If some treatment of a young animal makes that animal different from a control, it is reasonable to attribute the difference to the direct effect of the treatment. But the treatment might also act indirectly through its effect on the behavior of the parents. The only way in which a direct effect of a treatment can be distinguished from such an indirect action is by using artificial parents which are unaffected by the properties of the young; that is, by rearing the young on the equivalent of a bottle. This is practicable [671], but the method has evidently still to be used in studying the ontogeny of behavior. There are many possibilities to be investigated. For instance, Schaefer [578] has suggested that, if the temperature of nestlings is lowered, the female may be so disturbed that she secretes larger amounts of adrenal cortical hormones, and that these appear in the milk and thereby influence the young.

The preceding account ignores the uterine environment, but, as illustrated by DeFries and his colleagues, this is by no means a constant. Ovaries were transplanted between mice of different genotypes. As expected, the uterine environment influenced the growth rates of the young; but it also had an effect on behavior in an open field [190].

There is a well recognized behavioral effect of early handling which has not been satisfactorily linked with these experimental findings. This is taming. Wild rats, like many other undomesticated mammals, can be tamed by regular handling from an early age [47]. A tamed animal differs from an ordinary wild rat in withdrawing much less quickly from a human being, and in not struggling or biting when handled. As Ader [5] (for example) has shown, similar changes probably occur even when laboratory albinos are handled during their first three weeks after birth. Taming and allied phenomena exemplify the effects of familiarity: in general, harmless stimuli evoke progressively less attention as they are repeated. This phenomenon is discussed later under the heading of habituation (§7.3.2). The effects of handling early in life, however, operate on a longer time scale than those of typical habituation.

6.3.3 The Grandmother Effect

The outcome of interaction between mother and infant can involve a third generation. If we consider females of what we may call generation 0, it is easy to see how an environmental change which influences them could also influence their offspring (generation 1). But differences among females of generation 1 could in turn influence *their* offspring, that is, generation 2 (figure 59). This is not merely hypothetical. Cowley & Griesel fed rats of generation 0 on one of two diets: the experimental diet was low in protein (14 instead of 21 percent), and differed from the control diet in other respects. The "low protein" offspring (generation 1) made more errors in a test of problem-solving ability (§7.3.4.1) than controls whose mothers had received a normal diet; moreover, a deficiency in this respect was also present in the rats of generation 2 [177–8].

The plane of nutrition is not the only agency which could have this effect. Among other factors are environmental temperature, infection with pathogenic or symbiotic organisms, and various types of stimulation—discussed above—acting through the external senses [196]. The scope of such effects, including the number of generations which could be influenced, remains to be discovered. The demands on experimental design of researches in this field, which are heavy, have been discussed by Denenberg & Whimbey [197].

We must now summarize the general implications of the ontogenetic effects described so far. (Other effects on "intelligence" are discussed in §8.7.2.2.) First, the history of the subject illustrates the blinkered way in which experimental psychology was studied in the first half of this century. In 1922 Hammet [286] reported an effect of early handling on survival rate after parathyroidectomy, but this remarkable observation was followed up only a quarter-century later. The mere fact that minor differences of rearing can interfere with experimental findings is important for every scientific user of laboratory mammals. Its significance for wild mammals in natural conditions has still to be discovered. A grandmother effect has been postulated to account for the population cycles of *Microtus* and other small mammals [152]: as described in §5.3.1, these rodents develop a high population density, and then "crash"; the decline in fertility which follows the peak extends over two generations. If intense social interactions during crowding lead to low fertility, does the effect influence also the second generation? Such quasi-genetical effects could also occur in species whose populations do not fluctuate in this way.

Second, at present, the detailed information we have is only on laboratory stocks. Since these are often highly inbred, we need to know how homozygosis (§11.3) influences response to disturbance in early life. Inbreeding apart, the selection which laboratory stocks undergo could result in divergence from the wild type in this respect as in others.

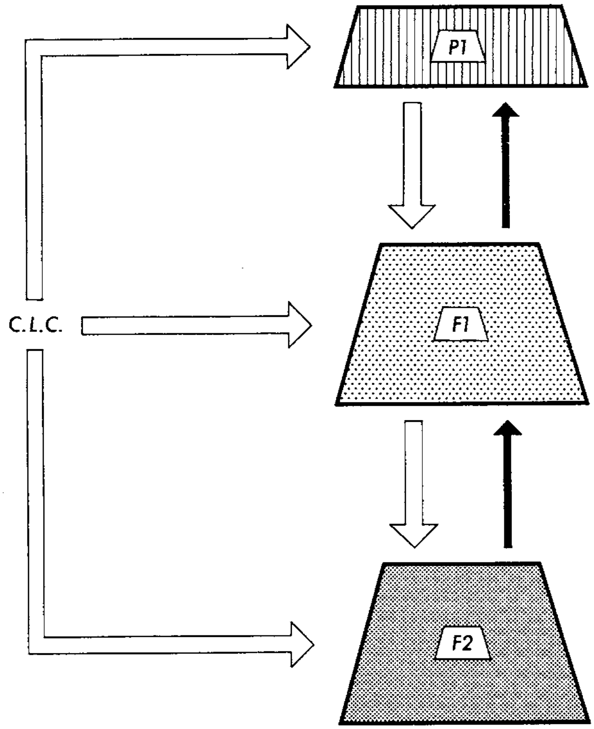


Figure 59. Diagram to illustrate action of a change of environment over three generations. Arrows indicate how breeding in a new environment could produce a cumulative effect over generations. A "feedback" from the young to the parents is also shown.

Third, there are questions of developmental physiology. The work on the endocrine effects of early treatments gives us the beginning of a physiological analysis. As experimental design becomes more rigorous, and analytical and neurological techniques more refined, we may expect a rapid increase in our understanding of environmental influences on the development of central nervous function.

Finally, as Daly [183] remarks, in all this work anthropomorphism or anthropocentrism are hazards which have not always been avoided. There is a tendency to regard a very quiet laboratory and a small cage as representing deprivation, when it may approximate more to the natural conditions of a burrow than does a complex, noisy environment. The domestication of laboratory rodents may have involved selection of genotypes which, unlike wild types, can thrive in conditions of chronic disturbance from human beings. The findings on the effects of varying conditions in early life on development will become generally significant when two things have been achieved: one is an authentic physiological account of the underlying processes; the other is application of findings on domestic animals in captivity to wild animals in their natural habitats.

Habit Formation: Methods

7

. . . we are justified in raising the question whether the concept of learning or of memory embraces a unitary process which can be studied as a single problem, or whether it may not instead cover a great variety of phenomena having no common organic basis.

K. S. Lashley

7.1 INTRODUCTION

A naturalist, Bagnall-Oakley, has described some events which follow occupation of a starling (*Sturnus vulgaris*) roost at Egmere in eastern England. Within a few weeks of the birds' arrival, large numbers of rats move into the earth banks nearby. The rats move about at night, and attack any bird that falls to the ground; a fluttering bird at once attracts a rush of rats from all quarters [30]. A similar observation has been described by Cottam. A large colony of rats lived in burrows near ponds and streams heavily stocked with fish. When food was thrown in the water, young fish congregated in great numbers. The rats learned to assemble at the same time, to eat scraps of food and to catch the fish. The rats swam "well and rapidly" [175].

In each chapter so far, reference has been made to such *changes in individual behavior due to stimulation*. The phrase emphasized is one definition of the term "learning" [676]. People who employ this definition (if any do) then use "learning" to refer to a kind of overt behavior. Another definition was given by a committee which debated the meanings of terms used in ethology: "internal changes which manifest themselves as adaptive change in individual behavior as a result of experience" [675]. Here the reference is not to behavior but to processes which, in a mammal, go on principally in the forebrain. In this and the next chapter we are concerned almost entirely with overt behavior. The word "learning" is not used: the different sorts of behavior it comprehends are very diverse, and it is doubtful whether they all should be brought together under the one term.

The terminology we use is a matter of convenience. The problems of studying behavior remain. We are now concerned with individual adaptation to a varying environment. Such adaptation is seen in the hypertrophy of organs—for instance, muscles or glands—resulting from use; but above all it is exemplified by changes in behavior which tend to keep an animal alive or to enable it to reproduce. It is this feature which leads to the use of the word "adaptive" in the second definition given above.

Since environments vary, the details of individual experience in the wild state are far from uniform even within a small population. Hence, as far as behavior is concerned, the diversity already present at fertilization is magnified and made more complex by the acquired adjustments of each individual. If cannon balls or guided missiles or planets had personalities of their own, and their behavior changed progressively in response to repeated stimuli, the subject of physics would present additional difficulties. Physicists would be obliged to make observations on vast numbers of individual objects and to construct case histories of each: they would then perhaps be able to predict the behavior of individual bodies (from previous observations of those bodies), but they would still be faced with the problem of grouping the individuals in classes concerning which more general predictions could be made.

This is the situation with which students of complex behavior have to cope. Consider superficially simple observations, such as those described in the first paragraph of this chapter. Or, better, we have more systematically reported observations such as those given in §4.2.2. A group of wild rats occupies a neighborhood. At one point in their range, a pile of food is put down every evening. The rats gradually adopt the habit of coming to this point every twenty-four hours, at a fixed time, and to make a substantial meal. There are, however, considerable individual differences in the behavior of the rats, even if we concern ourselves only with, say, adult males. How are we to investigate the development of a habit? Among the questions which may be asked are the following. (i) To what features of the situation is a rat responding during habit formation? (ii) Can the behavior be analyzed into distinct components? (iii) What internal states influence habit formation? (iv) What is its neurological basis? (v) How does the past history of the individual affect its ability to develop new habits?

The remainder of this chapter has two main sections. The first gives an account of laboratory methods of studying habit formation; some of the uses to which these methods are put are described, and so some of the findings from this type of research are introduced. The other section presents an unconventional classification of types of habit formation.

7.2 LABORATORY TECHNIQUES

7.2.1 Problems for Rats to Solve

7.2.1.1 *Discrimination apparatus.* It is hardly possible to make a systematic, experimental study of behavior as complex as that described at the beginning of the chapter. In practice, experimenters have usually employed situations which, structurally at least, are of the greatest possible simplicity. The animals are nearly always put in these situations for a brief period only—usually thirty minutes or less; these short exposures may be repeated at regular intervals of a few hours or days. This is a far remove from a natural situation. The experimental conditions are, in fact, often similar to those described earlier, in the discussion of "activity" (§3.2.1.1).

When an animal is free to move about a substantial area, at any given moment it seems to be able to choose, from a number of possibilities, what it will do next. If some goal object, such as food, can be reached only by a particular set of movements, the animal will probably develop the habit of performing these movements at regular intervals. This is so obvious that saying it may seem pointless.

We depart from the obvious only when we try to analyze the behavior. A feature of habit formation is a progressive loss of ineffectual movements: with repeated exposure to a situation, an animal comes to perform an economical motor pattern in a minimum time. At first there are many errors, or movements that do not lead to the goal; later, there are few or none. The loss of futile activity involves *discrimination* of different features of the surroundings. That is, the animal comes regularly to respond differently to different stimuli. This process, which is a component of all habit formation, can be investigated systematically only in a narrowly circumscribed environment.

Figure 7 illustrates equipment often used in experiments on discrimination. The animal, usually a laboratory rat, is required to leap a gap to one of two doors. The doors are differently marked, and the rat must use its eyes to distinguish between them. One door opens at a touch, and allows the animal to find food on a platform behind; the other is locked. In such a test of visual discrimination, the position of the two patterns—left or right—must be altered at random, so that the animal cannot solve the problem by developing a position preference, or by using visual information from the background. Another type of apparatus, circular and with a central starting platform, has been designed by Winefield & Jeeves; this can be used to eliminate background visual cues altogether [717]. The original "jumping stand" was due to Lashley [393], and in his experiments the rat fell into a net below if it chose the wrong door. This adds the complication of an apparent punishment for error, as well as reward for choosing correctly. The problems of reward and punishment must, however, be deferred to §8.3.

Whatever the precise design of the equipment, laboratory rats can be trained to jump reliably to one stimulus rather than another, even when tested in the presence of an unfamiliar audience of students. The training, however, requires patience; and initially the rats should be guided by hand ("shaped") and allowed to walk across a narrow gap.

Lashley's apparatus may be used to test animals for their ability to distinguish patterns, and also to study many of the complexities of habit formation, as we see in the next chapter (§8.2.3). One of its important characteristics is the simultaneous presentation of the contrasting stimuli. The same applies to the type of maze (a **T** or a **Y**) with a single choice point. Spontaneous alternation, described in §3.2.2, requires instant discrimination by an animal in such a maze.

Kimble [364] has reviewed the varieties of simultaneous discrimination, and also the alternative procedure of presenting the stimuli separately. Successive presentation usually requires the animal to restrain itself when one stimulus is presented, but to approach the other. Accordingly, it presents the animal with a more complex problem. Nevertheless, in natural conditions such discriminations must often be required.

7.2.1.2. *Mazes.* A natural environment has a complex structure, in which an animal may perform a variety of activities in quick succession. Small, at the beginning of this century, designed a semi-natural situation in his laboratory. Each rat was fasted. A box with a hole in it was put in the cage, and the hole covered with sawdust. The box, which was already familiar to the rat, contained food. The rat eventually found its way into the box, as a result of what Small describes as random scratching around in the sawdust. For one rat the time taken on first presentation was ninety minutes, but on the thirteenth presentation it was only thirty seconds [619].

In Small's experiments the rat had to find its way to a goal, but his design is too complex for the purposes of most experimental psychologists. Even a maze of the type shown in figure 60, made up of no more than a series of featureless, branching passages, presents difficult problems of interpretation, for the experimenter if not for the rat. The history of the use of mazes has been summarized by Munn [490] and by Mowrer [485]. At first, mazes were elaborate systems of pathways, like the famous one at Hampton Court where people spend a sunny afternoon getting lost; but eventually it became usual, for many purposes, to have only one choice point. A maze may consist of walled passages, of raised runways, or of canals filled with water. It may be variously illuminated or dark; in a featureless room or not; and in a sound-proof or a noisy one. Whatever the details, the animal is faced with one or more choices: in a complex maze of which it has had no previous experience, it gradually eliminates the alternatives, until the path from the start to the goal is run rapidly and with few errors and little hesitation (figure 70). During this process a rat may reach a stage when, at a particular point, it pauses and makes incipient movements, first in one direction, then in the other. This behavior has been called "vicarious trial-and-error" or VTE (reviewed by Mowrer [486]).

7.2.1.3. *Problem boxes.* Rats are well equipped to make their way through systems of tunnels or passages. But they also have some powers of manipulation, used in feeding (§4.2.3) and in nest building (§6.2.2). This sort of behavior, too, may be evoked in trial-and-error situations. Tolman has discussed experiments in which rats learn to get food by pulling a string [682, page 130]. Rats are allowed to feed from a pan, which on later presentations is slowly drawn out of reach; as the pan is removed, the rat seizes it and drags it back. Later, the only way in which the rat can get at the pan is by pulling on a string attached to it; it soon encounters the string while scrabbling for the pan, and learns to pull it, usually with its forefeet but sometimes with its teeth. Eventually, with the pan out of reach from the start of the experiment, the rat readily pulls it in with the string.

Once again, this interesting situation has proved inconvenient for experimental analysis. The most popular means of studying manipulatory trial-and-error behavior is the puzzle-box. That most used for rats (plate 24) was invented by Skinner [613]. Its essential feature, as we have seen, is a lever which, suitably moved, releases a pellet of food, a drop of water or other fluid or, in some experiments, switches a light or a current on or off. There may be two levers, and many other variations. An inexperienced rat in such a box makes a great variety of movements. Eventually, if moving the lever produces a suitable reward, it learns to press the lever without fuss.

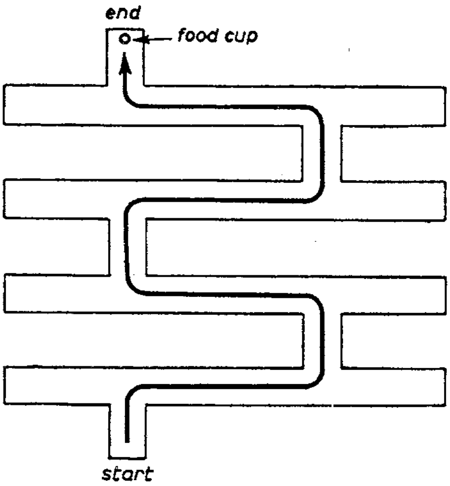


Figure 60. Plan of a typical enclosed maze. (After Tsang [686].)

The last statement is based on a comparison of what happens when pressing the lever leads to no reward. If pressing the lever merely produces a click, the rate of pressing remains very low. But the habit will develop even if pressing the lever yields a reward only occasionally. One of the features of the Skinner box is indeed the variety of "schedules of reinforcement" (reward) that it makes possible [235]. To make full use of these possibilities, an automatic, electronically controlled system is required, connected with the lever and with other features of the box such as signal lights, buzzers and so on. Instead of 100 percent reinforcement, such as a pellet of food for every lever-press, partial reinforcement may be offered: this could be, say, a pellet at every fifth press; or it could be a pellet delivered, on the average, on one in five presses, but at random intervals. There may also be a delay between pressing the lever and pellet delivery. One interesting type of schedule requires restraint by the animal: for example, the lever is pressed repeatedly until, on the tenth occasion, a light is switched on; the animal must now *stop* pressing the lever until, after five seconds, the pellet is delivered; if the lever is pressed during the five seconds, there is no pellet. Not only rats but even mice can be trained to do this. The reader can think of many variations on these themes. This, however, is an unprofitable exercise unless one has some new hypothesis that can be tested in this type of apparatus.

A disadvantage of the Skinner box (and of some other automatic equipment) is that, paradoxically, it leads to a neglect of behavior: the experimenter tends to pay attention to what is recorded on counters or revolving drums, and to ignore the behavior of the animal itself. The latter, when studied, sometimes proves to be unexpectedly interesting, if baffling. When, to obtain a reward, an animal has to stop pressing the lever, it may run around in circles or perform other movements [299]; in this, even inbred laboratory animals display much individual variation. A few workers have made detailed studies of the movements involved in bar-pressing. R. M. Herrick recorded the amount of work used. His rats showed much variation, and—unexpectedly—no tendency to minimize the effort expended [319]. A methodologically important finding has been reported by Renzi and his colleagues: in their experiments making the lever slightly less accessible than usual improved the rate at which a habit was developed [539].

7.2.1.4 *The shuttle box.* In the last-mentioned experiments a Skinner box was arranged so that a mild shock could be administered to the animal's feet. Onset of the shock was signaled in advance by a light: to avoid the shock, the animal had to press the bar when the light went on. Other apparatus, too, has been used for such avoidance learning. Warner used a cage in which shock, again administered through a floor grid, could be escaped by surmounting a small barrier and entering another compartment. In this case the shock was preceded by the sound of a buzzer, which was already known to produce no disturbance by itself. On the first experience of shock the rats made violent movements without specific direction; but quite quickly they learned, on hearing the buzzer, to cross the barrier with economy of effort and smoothness of movement [702]. Figure 61 gives a typical record. Bovet and his colleagues have described a fully automatic shuttle box based on the same principles. The equipment can be set to switch on a sound or a light at various intensities, durations and intervals; similarly, the characteristics of the shock can be varied. The relevant movements of the animal are automatically recorded [105].

Bovet-Nitti has reviewed the uses of this method and some of its findings. One of her examples (figure 62) gives the results of training laboratory mice to avoid shock. On each of five successive days, each mouse was given a session of one hundred trials. The mean percentage of successful avoidances of shock is shown, for each day, as a rectangle: by day 3 the percentage success was about 70, and by day 5 it was over 80. Superimposed on each rectangle is a graph which records performance within the session: each point represents the mean percentage success during a block of twenty trials. These graphs show that performance improved within each session; more interesting, they show an improvement *between* the first and second sessions, although the animals spent the interval in their home cages, not in the shuttle box.

This one example illustrates several of the possibilities, offered by this method, for the study of habit formation and of "memory": its advantages have been summarized by Bovet and his colleagues [104]. An important question is the severity of the effect of the shock. These authors refer to an experiment in which a home cage was connected to the shuttle box in which a mouse had been tested: "The mouse spontaneously returned to the shuttle box, presumably because of curiosity, in spite of the risk of receiving an electric shock."

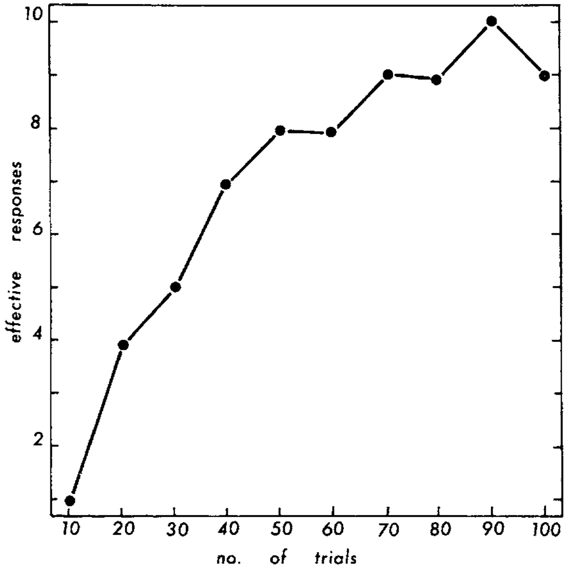


Figure 61. Avoidance of shock in a shuttle box. In this typical record, seventy trials are needed before 90 percent success is achieved. (After Mowrer [485].)

7.2.2 Conditional Reflexes

Each of the experimental conditions described in the preceding section abstracts certain features of a natural environment. In doing so, it makes possible study of particular components of complex habit formation. In the most famous of all techniques in this field, simplicity goes still further. The animal, traditionally a dog, is strapped in a harness, and cannot move about at all. This is the situation in which conditional reflexes (CRs) are usually studied. The adjective "conditioned" (commonly used in English) is a mistranslation from the Russian. Alternative names include "classical conditioning" and "conditional reflex type I"; the names arise because trial-and-error behavior, of the types described in the preceding sections, has also often been called "conditioning"; other names for trial-and-error include instrumental conditioning, operant conditioning, and CR type II [364]. In this book the term CR is used to refer only to the classical conditional reflex. The subject has been reviewed by Kimble [364]; and the researches on rats in which CRs have been studied have been summarized by Munn [490].

In the famous experiments by Pavlov (1899–1936) and his colleagues, the response studied was usually salivation. This, the unconditional response, is evoked by the presence of food in the mouth; accordingly, food constitutes the unconditional or releasing stimulus. This stimulus-response sequence seems to appear without previous practice. To prepare a dog for CR experiments is exacting and laborious [537]. Many months may be taken, during which the animal is habituated to the experimenters, the laboratory and the harness into which it has to be strapped. The training itself consists of repeatedly applying a new stimulus such as a sound or a light; this, the conditional stimulus, is presented at the time when the releasing stimulus is also applied or, more usually, a second or two before. The conditional stimulus must be one which, applied alone, does not evoke the response to be studied, or anything like it. A sound or a light serves well when salivation is being observed. The conditional stimulus must, however, produce *a* response: at first it is usually followed by a pricking of the ears, a turning of the head or some other sign of attention; this is the orienting response.

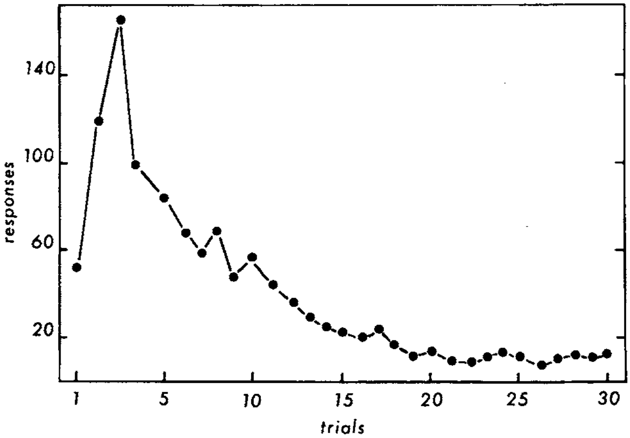


Figure 62. Acquisition of avoidance response. On each of five days mice had a session of one hundred trials in a shuttle box. Mean success for each run of twenty trials within sessions is shown by the points connected by lines; mean success for whole sessions, by the rectangles. There is evidence of improvement (a) within sessions, (b) from day to day, and (c) *between* sessions 1 & 2 and 2 & 3 (consolidation). (After Bovet-Nitti [106].)

Elementary texts often leave the impression that, as a result of training, "the response" to food comes to be evoked by the new (conditional) stimulus. This is not the case: the effects of training are much more complex. (i) The primary response to food includes not only salivation but also chewing and swallowing. Of these, only salivation is represented in the CR. (ii) A novel feature of the new response (salivation) is its relationship to the intensity of the stimulus that now evokes it: within limits, the magnitude of an unconditional response is proportional to the stimulus; for the CR, by contrast, there is an optimum intensity, and sufficient increase or decrease prevents the response (discrimination). (iii) Another feature of the new response is its time relationships: it is anticipatory. When the experiments begin, the sequence is: conditional stimulus (say, a sound), followed by unconditional stimulus (food), followed by salivation. After training, however, the sound is rapidly followed by salivation, whether the food appears or not; hence the new response is anticipatory: it occurs in advance of the time at which the original stimulus is applied. This still holds even when the delay is a minute or more: salivation occurs just *before* the time when the food is due. (iv) A further effect of training is that the orienting response gradually disappears; once training is complete, this response is wholly absent. (v) Other effects include changes in posture, in the heart and respiratory rates and in other features of behavior and physiology [34]. In particular, the conditional stimulus at first leads to increased heart and respiratory rates proportional to the intensity of the stimulus; with training, these responses decline.

Pavlov's method, despite its limitations, illustrated in a clear and quantitative way some general features of habit formation. (a) A first important finding concerns the rôle of the total sensory input. This is shown in experiments which demonstrate what Pavlov called external inhibition. To establish a CR reliably, the experimental conditions must be the same during both training and subsequent testing. If, when training is complete, an unfamiliar stimulus is applied at the same time as the conditional stimulus, the response usually fails. (In the early days, Pavlov's pupils were sometimes dismayed at the failure of a laboriously established CR when the professor himself was invited to observe it. This led to the design of a laboratory in which the animals under training could be observed without being disturbed.) The animal is in fact affected by the total situation: it is not a machine set going by the pressing of a switch.

(b) The second principle is a truism, but nonetheless important. The animal's internal state determines which ones, from among its repertoire of possible responses, can actually be evoked. If the salivary response to food is to be studied, the animal should be fasted for some hours beforehand.

(c) The third principle is related to the second: the CR is lost if the conditional stimulus is repeatedly presented, over a short period ("massed trials"), without the unconditional stimulus. This has been called "internal inhibition"; but it is now usually (but less appropriately) named extinction. It is, again, a matter of everyday experience. It is also to be expected if one considers the function of the CR, for it is no use salivating if there is no food. Extinction, then, is a corollary of the relationship between the animal's internal state and the releasing (unconditional) stimulus.

(d) G. B. Shaw once complained that the study of CRs yielded nothing but statements of the obvious [602]. That he was wrong appears when extinction is examined further. Suppose that a CR is extinguished, by repeated presentation of the conditional stimulus without reinforcement, on one day. If, on the next day, the conditional stimulus is presented again, the response reappears. The animal behaves as though it has forgotten that the response to the conditional stimulus is no longer rewarded. This spontaneous recovery shows that extinction is not a mere reversal of the neural changes due to training: evidently, the CR is due to one set of neural processes and extinction to another. (Hence follows the superiority of the term "internal inhibition" for this process.)

(e) Pavlov's work was explicitly designed to throw light on the physiology of the cerebral cortex. Nevertheless, we still know little of what goes on during the formation of a conditional reflex. A beginning, however, has been made in work in which the electrical activity of subcortical structures has been recorded during establishment of a CR [345, 424]. The unconditional stimulus, in some of the experiments, was a flickering light: this induced a neural discharge of a specific frequency. A sound was used as a conditional stimulus; once training was complete, the sound alone evoked the pattern of discharge previously due to the light. This conditional discharge appeared in the midbrain reticular formation (§2.5) before it was evident in the cortex; it was also stronger in the reticular formation, and longer-lasting there on each occasion on which it was evoked. These observations illustrate the way in which the cerebral cortex interacts with other structures during habit formation.

We must now compare the CR with the various sorts of trial-and-error behavior described in §7.2.1. The CR is typically a component of a preexisting response: salivation is one feature of eating. During formation of a habit by trial-and-error, many inappropriate movements have to be made and eventually discarded. But, provided the animal is allowed freedom of movement, trial-and-error permits a much greater degree of novelty in the response. The ultimate pattern is an economical system of movements which, as a whole, is new. It may include CRs; for instance, finding food in a maze, or getting it in a puzzle box, must involve many proprioceptive and other reflexes and must end with salivation.

An important difference of trial-and-error from the CR is the time relationship with the reinforcing stimulus. At all stages during trial-and-error, the response eventually acquired must be made before the reinforcement. Hence the response is said to be *instrumental* in bringing the animal to its reward. As a corollary, trial-and-error is sometimes said to differ from the CR in altering the circumstances of the animal: once the animal hits on the right response, it is enabled to make a specific change in its environment. But this distinction is not wholly valid: for instance, the saliva secreted by the Pavlovian dog dissolves some of the food and makes it more digestible [309].

A final, important feature of CRs is that they are usually mediated by the autonomic nervous system. This limitation is partly imposed by the conditions of the experiments: if an animal is so tied up that it cannot move, the activity that remains to be recorded is inevitably only reflex; and the reflexes most readily quantified are those involving smooth muscle or glands. If the harness is removed, the animal's behavior becomes much more complex, and may include walking about in response to the conditional stimulus. But, as Zener [736] has pointed out, the response elicited by the conditional stimulus is still only fragmentary. Chewing rarely occurs: the dog does not eat imaginary food.

A study by Ellison and others reveals some of the contrasted features of CRs and trial-and-error (or instrumental) behavior. Dogs were trained to stand in a harness and to press a lever ten times at the onset of a conditional stimulus (usually a light). At the tenth press the light went off and a second conditional stimulus (a sound) came on; eight seconds later food was presented. There were consequently two stages before eating. (i) During the first: (a) the animal pressed the bar; (b) high activity was recorded in the pyramidal system (§2.3.1); (c) the heart rate was high; and (d) there was increased activity in the reticular system (§2.5). (ii) During the interval between offset of the first conditional stimulus and the arrival of food: (a) the animal did not press the bar; (b) pyramidal activity was low; (c) the heart rate declined; (d) reticular activity remained high; (e) salivation occurred in the classical, Pavlovian manner [216]. This is an example of the way in which a CR can be an element in a complex habit; it also shows how the neural processes which accompany habit formation can be analyzed.

The CR occupies a curious place in history. A correct account must be highly technical, and should bring out both the limitations of the method and the complexities of the changes which take place during training. Yet the expression "conditioned reflex" is part of common speech. Shaw [602] ridiculed both CRs and Pavlov in a brilliantly entertaining polemic. And Bertrand Russell [569], the outstanding philosopher and polymath of the age, wrote: "We may take the conditioned reflex as characteristic of life, especially in its higher forms, and above all as characteristic of human intelligence." This misleading statement is echoed in many standard physiological texts: in these works it is customary to end the chapters on the brain with a summary, usually garbled, of Pavlov's work, without mentioning other kinds of behavior. The true general importance of Pavlov's work is in its physiological frame of reference. It has made possible systematic, objective and rigorous studies of features of habit formation even by such large-brained animals as dogs. It has also helped to reveal the complex autonomic processes which accompany the changes in the forebrain. Despite this, the great mass of laboratory research on the "laws of learning" has necessarily been on animals in trial-and-error situations: mazes, problem boxes and the like (§7.3.4; chapter 8).

7.3 CLASSIFICATION OF ADAPTIVE BEHAVIOR

7.3.1 The Problem

In both scientific writing and ordinary speech the word "learning" has many meanings. If we take it to refer to observed behavior, and not to internal processes, the kinds of behavior it covers are still diverse. The rest of this chapter classifies the items of adult behavior commonly said to be due to learning. The headings below are abritrary: they merely represent groups of experimental findings which are conveniently described in separate sections. There may be neural processes common to all of them, but this has still to be established. One important category is omitted here: special features of the behavior of young animals, and the effects of early experience on adult behavior, are deferred to §8.7.2.

7.3.2 Habituation

Habituation is defined in this book as the waning of a response on repeated stimulation. Just as a change of stimulation tends to arouse an animal (§3.2.1.3), so continued or repeated exposure to a constant stimulus leads to a decline in the activity at first evoked. Habituation, so defined, includes "negative adaptation"; this refers to decline in reflexes and other simple responses. A rat jumps if it hears a sudden, high-pitched noise. Prosser & Hunter evoked this startle response by means of a click, sounded at intervals of fifteen seconds in a sound-proof room; the response was measured by electrodes in the leg muscles. After thirty clicks the response declined; during another thirty-five it was irregular; eventually it disappeared [531]. Another kind of example has been described in §3.3: the avoidance of a new object by wild rats fades with prolonged exposure to the object.

Throughout the animal kingdom one can observe habituation of movements of withdrawal and of other protective responses such as the eye-blink. These movements diminish when a stimulus is repeated, yet not followed by injury or further disturbance. Habituation is also a necessary component of more complex activities. When a wild rat first encounters food in an unfamiliar place, it must lose both its avoidance behavior and also its tendency to explore generally, before it can form a regular habit of visiting the food with a minimum of effort.

It may be asked how we can distinguish "true" habituation from fatigue. To answer, the question must be re-formulated. The definition of the term "habituation" given above includes phenomena which would commonly be called examples or consequences of fatigue; if this is disliked, the definition must be altered. As Haldane [279] has pointed out, students of behavior tend to call the waning of a response "habituation" if they approve of it, "fatigue" if they do not. It is more useful to ask: Are there different kinds of habituation (as defined); and, if so, is one kind a result, say, of the accumulation in muscles of metabolites, another a consequence of changes in sense organs, and yet a third due to changes in the CNS?

Sensory accommodation is fully described in textbooks of physiology. Recovery from it is rapid. If it were not, the sense organs would be out of action most of the time. Recovery from the sort of action exemplified above usually takes longer: while a sense organ often recovers in a few seconds, habituation of the startle reflex, to the criterion of no response to five successive stimuli, is usually followed by complete recovery of the response in about twenty minutes [531]. Askew and his colleagues have made a detailed study of headshaking by rats, induced by a puff of compressed air directed at one ear. The response is readily abolished by repeated stimulation. When rats so treated were given thirty minutes' rest, and then stimulated again, the response reappeared, but not fully. After six hours' rest there was little effect of the "training"; hence in this case the habituation was specific to the sense organ affected. If, after habituation, the opposite ear was stimulated instead, the full response was evoked [28].

Prolonged habituation is due, not to the accumulation of metabolites in muscles, but to processes in the CNS. If repeated stimulation has abolished a rat's startle reflex, an additional disturbance such as a flashing light at once restores at in full [364]. Evidently the loss of the reflex is independent of any important decline in muscular responsiveness: the change must be central, and indeed probably in the forebrain and reticular formation (§2.5; figure 12). A repeated stimulus loses its effect on the reticular formation, just as it does on overt behavior. If the stimulus to which the animal is habituated is a tone of given frequency, the sounding of another frequency produces a full response in the RAS; so does a stimulus, such as a puff of air, which affects a different sensory modality. Sharpless & Jasper have produced similar habituation to a simple melody or "pattern of several tones"; when this is established, sounding an isolated tone from among those that form part of the pattern causes activation of the RAS. Here then is a neural counterpart of the behavioral phenomena described above [601].

7.3.3 Autonomic Habits

Habituation is a component of all complex habit formation. Similarly, visceral responses, such as changes in digestive secretions, sweating, heart rate, and the activity of smooth muscle, accompany all behavior. What we observe as behavior is mainly a product of the skeletal musculature and is regulated by the somatic motor output of the CNS, while visceral changes are regulated by the autonomic nervous system. Pavlov was able, as we saw above, to study changes in visceral habits by preventing his animals from making any major skeletal response. In his classical conditional reflex of salivation, a visceral component of more complex behavior comes to be evoked by a stimulus which at first has no effect on it. Alternatively, as Schoenfeld and others have shown, the initial effect of the conditional stimulus may be the opposite of the conditional response. They used rats, and light as a conditional stimulus. At first, the light induced a slowing of the heart rate; but, as a result of being paired with the offer of milk, it came to evoke acceleration instead [583].

Any one of a variety of visceral responses can be used in the way in which Pavlov used salivation [364]. In all such experiments, some form of the response studied is already evoked by an unconditional stimulus: food in the mouth induces salivation, and so on. During the 1960s N. E. Miller and his colleagues added a new dimension to the study of visceral habits. One question asked by Miller was whether an animal could be trained to alter visceral activities quite independently of skeletal responses. Accordingly, experiments were carried out on rats treated with a drug of the curare group. These drugs produce complete paralysis of the skeletal muscles, but the input to the CNS from all the senses is unaffected. (A man treated in this way is unable to speak or move, but later can report on the events which went on around him during the paralysis.) In these conditions the usual type of reward, such as a fragment of food, cannot be used. Instead, the reward was brain stimulation (§2.2.3). A light or a sound was used to signal to the rat that this reward was available; and the brain stimulation actually occurred if the rat altered its heart rate. In some experiments the animals were required to increase the heart rate, in others to reduce it. After many difficulties had been overcome, rats were successfully trained to alter their heart rates to achieve this type of reward. Among the difficulties, Miller remarks, was the belief of his graduate students and research assistants that the task was impossible [463]. In further experiments rats were trained to alter their heart rate in order to avoid receiving a slight electric shock to the tail.

Similar results were obtained when the change required of the animal was in the activity of the gut. A balloon filled with water was installed in the large intestine, so that its movements could be recorded. Animals were then trained to increase or to reduce peristaltic movements in order to achieve brain stimulation. Alterations in heart rate and in peristalsis could be induced independently. Indeed, some experiments showed a remarkable localization of response. Curarized rats were induced, by the means already described, to increase the dilation of the blood vessels of one external ear alone. There were no accompanying changes in vasodilation in the skin of the forepaws or tail [201–2, 464].

In further experiments, DiCara and others found it possible to induce Pavlovian conditional reflexes of the heart beat and intestine in rats of which most of the cerebral cortex had been removed; but the type of "instrumental conditioning" described above could be achieved only if the animals had intact brains [200].

7.3.4 "Intelligence"

7.3.4.1 *Measures and Definitions.* A non-technical but agreeable classification of habits is into two classes: (i) simple; (ii) intelligent. Becoming accustomed to a noise which at first disturbs us (habituation) is not regarded as a sign of "intelligence"; nor is salivation at the sight of a lemon; nor is solving an irritating puzzle by a series of "random" movements. But if we solve a problem by insight into the relationships of its parts, or by putting together two hitherto separate items of knowledge, we call that intelligent. When a simple habit is developed, a particular response, or absence of response, gradually becomes associated with a specific situation. The behavior we call "intelligent" is more difficult to define, to describe or to analyze;

nor is it sharply distinct from simple habit formation. But it presents problems conveniently discussed separately. The term "intelligence" resembles "instinct" and "drive" in having been used so vaguely and variously that it may seem better to avoid it. But, even if this is granted, we are still obliged to master the facts.

Many of the relevant facts concern problems of measurement. A first difficulty is the many agencies at work. Early studies on differences among rats in problem solving ability involved the selection, from a mixed stock, of genetically different strains (further described in §11.2). In one celebrated investigation, the score in learning a maze was used as a criterion of "brightness" or "dullness" [685]. Scores so derived reflect a complex of factors, from the degree of need (for instance) for food at the time of testing, through early experience or training, to sensory equipment and genetical constitution. All three could act on features of behavior, such as exploratory tendencies or the avoidance of strange objects, which might influence ability.

A second difficulty is in devising a scale of measurement. When the intellectual abilities of people are to be compared, the subjects are set a series of problems of increasing difficulty. Difficulty is assessed by the proportion of individuals capable of solving a problem, either in the population studied or in a standard group. Some problems must be soluble by almost all, some by hardly any individuals. The criterion is then a function both of the predilections of those who design the tests and of the standard population. There is no independent scale of "intelligence" comparable to that, say, of weight-lifting ability.

A third difficulty, related to the first, is that of disentangling "pure intelligence" from other qualities which influence its expression. A problem must present a goal, and a goal implies "motivation"; that is, the subject must be in a state which accords with the reward offered on solving the problem. (This holds even if the reward is only the operation of solving the problem.) When testing "intelligence" it is usually held desirable to keep the factor of internal state constant. This is because it is commonly assumed that there is a quality ("intelligence" or "IQ" or some such thing) which is independent of "motivation"; but such an assumption cannot be justified.

We now consider some relevant experiments on rats. A number of investigators have studied the ability of rats to learn a maze in which the correct route requires double alternation of turns (reviewed by Munn [490, page 283]); that is, the rat has to go right, right, left, left, right, right, and so on. The conditions should be carefully arranged so that the rat cannot distinguish different points in the maze by means of irrelevant cues, such as different echoes from below the runway; it then usually fails to get beyond r, r, l, l. There are, however, examples of a probable learning of double alternation in some form. Evidently, this sort of task is on the borderline of ability of laboratory rats.

Another kind of task, also difficult for rats, is the oddity problem. The animal is required to approach one of three objects or patterns; the correct one is that which differs from the other two. Monkeys can easily learn to do this. For some time it was thought to be beyond a rat's powers; but eventually Wodinsky & Bitterman used rats with much previous experience of problems which required them to jump toward one of three windows. (Figure 7, illustrates the type of apparatus used, but one with only two windows.) The rats had been trained to switch readily from (i) choosing a black card in preference to either of two white cards to (ii) choosing a white in preference to two black ones. When, after this, the problem was to choose always the odd card (whether white or black), the rats quickly learned to do so. Other rats learned comparable tasks [719].

In solving the oddity problem, rats have to abstract, in each situation, a general property of the objects presented: instead of responding to particular objects (shapes, textures or odors), they have to be guided by the difference (any difference)—of one object from two others. In human affairs we consider it "intelligent" to identify a common formal structure in a number of disparate phenomena. A further class of examples is found in the response to numbers, that is, the ability to respond to the *n*th of a series of objects or events, regardless of what the objects or events are. Chen asked the question whether rats can count: he required his animals to run around a circular passage a specific number of times (from two to seven) for a reward; the size of the circle was sometimes varied, so that time spent or distance traveled could not be used as a clue; and in some experiments the runway was altered to an approximate ellipse, to change the proprioceptive input which resulted from running. A number of rats were successfully trained in this way. An incidental observation concerned behavior at the entrance to the passageway in which the reward was given: while circling, "the animal would usually come to a stop at the entrance, swinging its head toward the stem or standing still for a moment, before starting the next turn" [150].

The experiments so far described in this section illustrate the plural character of "intelligent" behavior: a variety of abilities is involved. They do not provide a scale suitable for measuring ability that varies over a wide range; but the best known "intelligence test" for rats does so. During an inquiry into the effects of early experience, Hebb & Williams [312] trained rats to find food in one of four containers in an open arena. This procedure revealed no difference between two groups of rats. The task took a long time to learn and, in Hebb's words, presumably should "be classed as rote learning rather than insightful" [307]. The "intelligence test" was designed to overcome this difficulty and, when applied, showed a clear difference. The new method, as revised by Rabinowitch & Rosvold [533], is illustrated in figure 63. A series of tests is set, each in the same apparatus. Each item is a detour or *Umweg* problem which can be quite quickly mastered by a rat. Each rat must be accustomed to the apparatus, to being handled and to eating in the food box; when all this has been done, the rat is given preliminary runs which are not used in scoring. The period of fasting is standardized, and so are all surrounding circumstances. The method is reliable, in the sense that re-tests give closely similar scores to original tests.

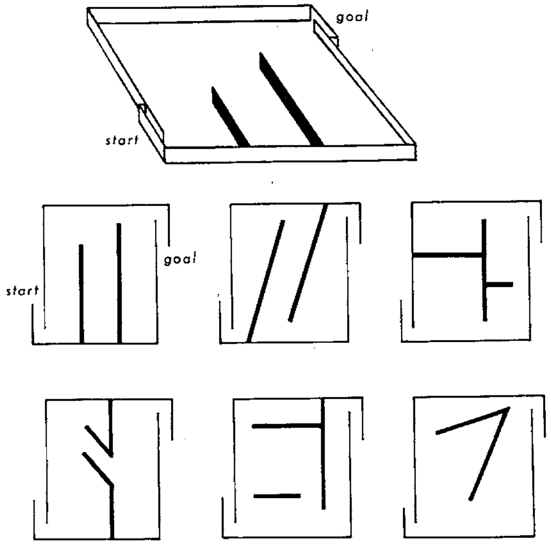


Figure 63. "Intelligence test" for rats. Above, an enclosure with movable barriers. The remaining diagrams show different arrangements, each of which presents a detour problem. (After Hebb & Williams [312].)

7.3.4.2 *"Insight" behavior.* Despite Hebb's remark, animals tested by the Hebb-Williams method have little opportunity to display "insight" behavior. Several formal definitions for this term have been proposed. One, slightly shortened, is: the solution of a problem by a sudden reorganization of behavior. Another is: a gross difference in behavior on successive presentations of a problem, when the behavior on the second occasion is judged by the experimenter to be efficient. The latter, based on one by Verplanck [693], is perhaps unnecessarily cynical. In this book, the first definition is used, despite its vagueness.

In any case, no definition is as informative as a full description of what actually happens. As with trial-and-error, we are dealing with problem-solving. An animal is faced with a situation in which, we know, it will carry out some act, or achieve some end-state, if it can. The goal, as usual, is determined by the animal's internal state, which may be any one of a number of deficits. To reach its goal, the animal must perform a series of movements which it has not performed before: even though it has already carried out the component parts separately, it has never before achieved the total pattern. We have seen how an animal may solve a problem by a series of initially ill-directed movements, and that these movements are not random in a strict sense. One factor which reduces randomness is previous experience: in problem-solving, an animal's performance may be much or little influenced in this way. In an extreme case an animal may perform the appropriate act without delay, error or unnecessary exertion, on its first exposure to the problem. It is, of course, making use of previous experience—experience, that is, of different elements which now make up the total situation; its behavior then depends in part on the unobtrusive storage of information that has taken place on earlier occasions, and not on any overt trial-and-error.

The traditional examples are those in which a monkey or ape employs tools or manipulates a puzzle. Rats are less dexterous; the problems which best allow them to display insight behavior are presented by mazes. Figure 64 illustrates the principle of a series of classical studies by Maier. Each rat is allowed to learn different parts of a maze on different occasions, and under different deficits. Each part of the maze has a different kind of flooring; this makes use of the highly developed sensitivity of the skin of a rat's toes. While the habit of running in one part of the maze is being developed, the other parts are blocked. For instance, rats may be trained to run to both H and U (in the diagram) for water. They are also trained to run from R to X for food; and they are allowed the experience of moving between X and U. In the test of "reasoning" (as Maier called it) the rat is faced with a new situation: it has been fasted; it is put at a starting point (R) from which it can go left or right; both these paths have previously, on different occasions, led it to water, but from only one of the water points (U) is it possible to go further to food. Maier's rats chose the correct route more often than the wrong one [428]. In doing so, they made use of separate previous experiences, to make the correct movements on their first encounter with the problem.

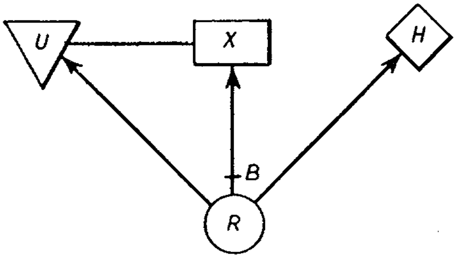


Figure 64. Complex habit formation: the principle of Maier's experiments on "reasoning" by rats. A rat learns different parts of the apparatus on different occasions and later makes use of the separate experiences to solve a new problem. See text. (After Hull [337].)

In further experiments, Tolman & Honzik, and later others, used the design of maze shown in figure 65. Rats first experienced the maze with all paths open, and learned to take the direct route to the goal. When this path was blocked at A, they learned to take the shorter of the two remaining paths. The test was to block the direct route at B, and so to leave only the longest route open. In the original study, fourteen out of fifteen rats took the longest, but only open, path [683]. Later, however, Dove & Thompson repeated this experiment with some modifications and with equivocal results: most of the rats failed on the first trial, but succeeded on the second or third trials; this suggested rapid learning by trial-and-error. In further experiments by these authors the blocks were made conspicuous by painted lines which could be seen from the choice point. No animal then chose the long route on any of the test runs. Evidently it was being checked at point B, during a run on the straight path, that led to the choice of the long path [208].

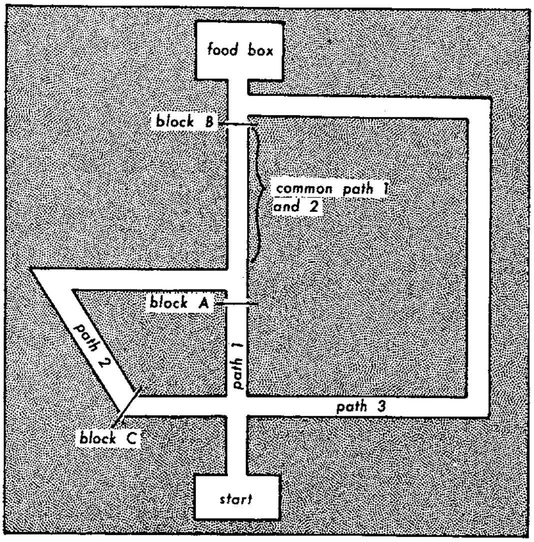


Figure 65. Complex habit formation: the modification by Dove & Thompson [208] of the Tolman-Honzik maze. See text.

Clearly, the conditions in which rats unequivocally display insight behavior are narrowly limited. But this conclusion must be qualified. The experiments of Maier and of Tolman & Honzik were designed to show insight behavior in a form in which it could not be confused with trial-and-error; but much of the behavior which contains an insightful element also involves some trial-and-error. In trial-and-error behavior in which previous experience plays little part, the habit develops in the manner illustrated in figure 61. This contrasts with what happens when exploratory learning is effective: the response is acquired much more quickly—sometimes rather suddenly; this is exemplified in the second group of experiments by Dove & Thompson mentioned above.

We must now examine further what is meant by "behavior which contains an 'insightful' element" and similar vague phrases. The main reason for imprecision is evident enough: the behavior is difficult to describe and to classify in a few words. This is partly due to the attempt to distinguish two phenomena which are in fact not distinct. The clearest forms of trial-and-error are admittedly quite different from the sudden, smooth and novel solution of a problem of classical insight behavior; in the latter, one gets the impression that, by contrast with trial-and-error, the solution *precedes* the movement which brings the animal to its goal: it is as if the animal has thought out the answer before moving (perhaps by an internal process of trial-and-error). The difficulty arises when one examines performances that lie between these extremes. The exploratory learning displayed in the acquisition of maze habits (§ 3.4.1) and similar tasks intrudes an apparently alien element in situations in which plain trial-and-error might be expected. The same applies to "learning set" (discussed later in § 8.4.2). We must evidently expect, in any example of complex habit formation, features both of trial-and-error and of "insight"; this may be inconvenient, but it serves to remind us that natural phenomena are always more subtle and multiplex than the words we use to describe them.

Habit Formation: Analysis

8

A little learning is a dang'rous thing;
Drink deep, or taste not the Pierian spring;
There shallow draughts intoxicate the brain,
And drinking largely sobers us again.

Alexander Pope

8.1 INTRODUCTION

The preceding chapter lists categories of habit formation, although these categories are better regarded as components of most habits. The question whether there is a single, underlying process of "learning" is left open, until more is known of the neural basis of the behavior. Whatever classification we care to use, our categories reflect different experimental procedures as much as they correspond to the facts of what animals do. Nevertheless, there is much to be studied in the regularities of overt behavior alone. Most of this chapter is, accordingly, devoted to the analysis of trial-and-error behavior, or instrumental (operant) conditioning [364].

8.2 STIMULI

8.2.1 Sensory Modalities

The behavior of all animals with nervous systems is mediated by links between sense organs and effectors. Habit formation depends on the creation of new links. We now ask whether all sense organs can take part in this process: that is, whether *any* kind of cue can be involved in a new association with a response. In most relevant experiments the cues are chosen for the experimenter's convenience. Visual and auditory stimuli (within certain ranges) are easily observed and presented, but not kinesthetic or olfactory. Neglect of the preferences and limitations of experimenters can lead to error. An easily ignored sensory capacity is the ability to respond to sounds of a pitch too high for man. Animals that can respond to such sounds often also produce them. They may then (i) act as social signals, (ii) serve in echo-location. Small mammals are usually nocturnal, and so a non-visual method of locating objects at a distance is appropriate for them. The whole of this subject has been admirably reviewed by Griffin [271]. Rats are among the species that produce "ultrasonic" sounds [16, 598–99]; and blinded laboratory rats can use echo-location while learning to run a maze [547].

It is not difficult to grasp imaginatively that other animals respond to sounds beyond our hearing, and echo-location by sounds of moderate pitch is used by blind human beings; but comprehension of the "olfactory world" of an animal such as a rat is far more difficult. As we know, odors play a major part in mating and other social behavior (§§ 5.2.3; 6.1.2), and rats readily make use of odors in finding food (§ 4.2.1.1). Ritchie has further shown how important and even disconcerting such stimuli can be during experiments on habit formation: he was concerned with the question whether rats find their way about by (i) learning to make particular movements, or (ii) responding to particular objects in their surroundings; eventually the rats in his experiments were found to be directing their movements by means of the odors and sounds from other rats caged nearby [548].

In general, then, any exteroceptors can mediate in habit formation, and they do so according to their own range of sensitivity, which is often very different from ours. The central nervous system has, however, also internal sources of "information"; these too can supply cues for learning. Blinded rats can discriminate inclined planes differing in slope by only ten degrees, and some can distinguish differences of only four degrees. Hence, if rats are run in a maze in which the pathways have different inclinations, they learn more rapidly than in one of the same pattern in which all pathways are level. Rats can also be trained to select the turning that is a particular distance from the start, with no cue other than distance. These are examples of the importance of kinesthetic cues [628]. Further, as we saw in § 3.2.2, spontaneous alternation is usually based on visual differences between the alternative paths; but in certain conditions it is possible to demonstrate response alternation, in which the cues are evidently proprioceptive. In a number of studies, reviewed by Bindra [94, page 181] interoceptive cues too have been shown to be the basis of a habit: rats can be trained to avoid a shock by taking one path when they are hungry but another when they are thirsty, even though they receive neither food nor drink in either path.

8.2.2. Cues and Direction-Finding

Any input to the CNS can, then, serve as a cue or conditional stimulus for a new habit. In any situation which offers a number of cues, affecting different senses, it is impossible to say *a priori* which actually evoke the animal's responses. There has, indeed, been controversy on just what sort of cues a rat employs in learning a maze. Is it learning to make a particular series of movements? If so, the process may perhaps be described in stimulus-response, or SR, terms: that is, it consists of learning to make one particular movement to the stimulus situation at the starting point, another at the next point, and so on. This formulation has been proposed especially by C. L. Hull [338–9]. But no such theory can account for all performances in mazes or in other problem-solving. Early evidence was reviewed with elegant lucidity by Lashley [392]—lucidity which, unfortunately, few writers on behavior contrive to imitate.

One kind of observation, inexplicable in simple stimulus-response terms, concerns learning to respond to a pattern: the pattern may in principle be visual (a shape), auditory (a tune) or, presumably, tactile (a shape again)—though we know little about the last, apart from some work on *Octopus* [730]: in most experiments it is visual. As we saw in § 7.2.1.1, a rat may be trained to jump on to a platform toward a particular shape; and the precise shape can be varied to some extent without interfering with the response. This is an example of generalization (discussed also in § 8.2.3). Familiar examples in ourselves are the recognition of letters printed in different type faces and of sentences spoken in different accents: each member of a series of events may be clearly different yet display a particular system of relationships, or pattern, in common. Another kind of example is the result of training an animal to make a brightness discrimination with one eye covered; on completion of the training, if the animal is tested with the trained eye covered and the other free, the discrimination is still made.

On the motor side, correspondingly, we find response generalization. Rats trained to run a maze make their way through it thereafter without repeating exactly the same movements: if the maze is filled with water, they will swim through it; if, after training, they have operations that damage the cerebellum and so cause motor inco-ordination, they will virtually roll through it. Dodwell & Bessant trained rats to swim through a water maze. Some had previously been run passively through the maze on a trolley; these did better than controls which had not had this experience. After the first three or four runs on the trolley, the rats anticipated the next turn by moving their heads; and, as the goal box was approached, they moved to the front of the trolley or even jumped into the water. Here is an example of acquiring an ability without performing the activity (swimming) which makes the process evident to an observer [204].

Accordingly, some workers have supported the view that, in learning a maze (for instance), a rat or other mammal is learning a set of relationships, just as a man does when he becomes able to carry a map in his head. Tolman does indeed write of "cognitive maps" when describing the achievements of rats [681]. This phrase illustrates how difficult it is to describe some complex behavior except in imagery based on human experience. We know as yet hardly anything of the underlying neural processes; no doubt, when we do, our language will become more precise.

Theories of place-learning and response-learning have often been treated as alternatives, but both processes certainly occur [485–86, 514]. The cues for habit-formation, as we saw above, can be of all kinds. Two further groups of experiments, on direction-finding by rats, support this conclusion. The first comprises those which deal with exploratory learning, already described in § 3.4.1. The essential features of this process were first made clear by Blodgett [99]. Rats put in a maze which contains no reward simply move about. If, later, they are run in the maze with a reward of food at the goal, they learn the route more quickly than controls with no unrewarded experience of the maze: they make fewer errors and their running time is shorter (figure 66).

The same effect is observed if animals are run for a series of trials when satiated, but with the reward present; they do not then develop the habit of running rapidly from starting point to goal, but the habit is rapidly developed if they are later run after fasting. Despite some controversy, there is no doubt of the reality of exploratory learning [39].

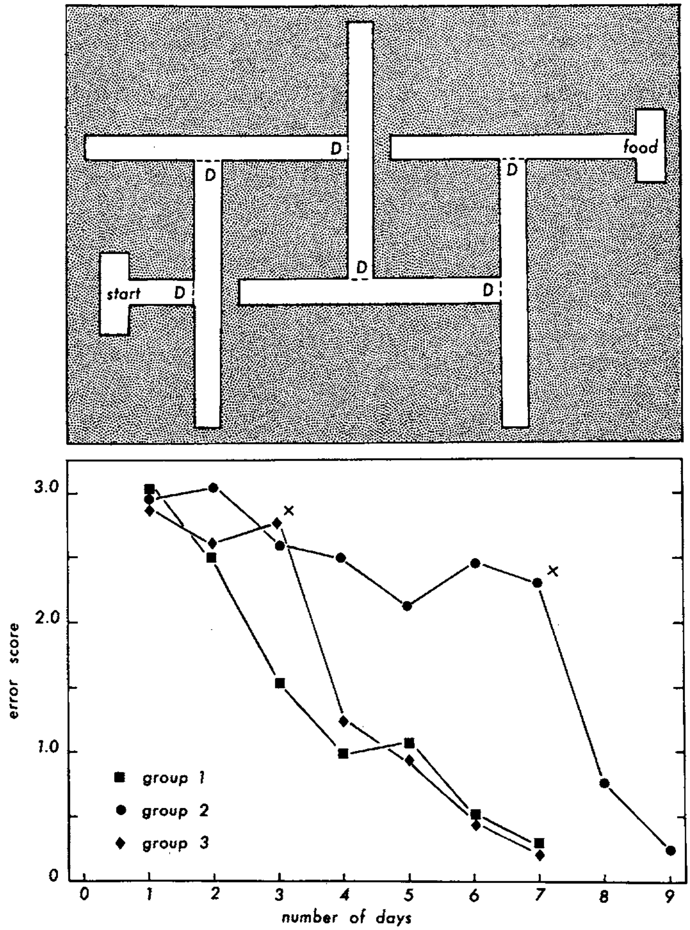


Figure 66. Exploratory (latent) learning. Above, plan of maze used by Blodgett. (D = doors which were closed behind the rat as it moved from start to goal.) Below, error scores of three groups of rats. Those of group 1 were trained when fasted in the usual way, with food in the goal box on each run; their curve of habit formation is typical. Rats in the other groups were not at first rewarded; but, at point X, reward was introduced: this led to a sharp reduction in errors, attributable to previous exploratory or latent learning. (After Blodgett [99].)

The rapid learning of a maze due to previous exploration is an example of insight behavior as defined in § 7.3.4.2. It does not, however, tell us anything precise about the stimuli, external or internal, to which the animal is responding. The question of direction-finding has been studied further in a "sunburst" apparatus (figure 67). Rats in this situation choose most often the one out of eighteen possible paths which leads them directly to the goal, even though they have previously learned to reach the goal from a quite different quarter. The rats behave as though they have a "sense of direction" [97]. This sort of experiment, originally carried out by E. C. Tolman and his colleagues, has been repeated by others. Success evidently depends on the existence of cues outside the maze itself: as we saw above, rats can orient themselves on all sorts of directional stimuli. Evidently, rats sometimes behave like men remembering a map or plan or the layout of a system of relationships previously experienced. Hence habit formation cannot be adequately described in simple stimulus-response terms.

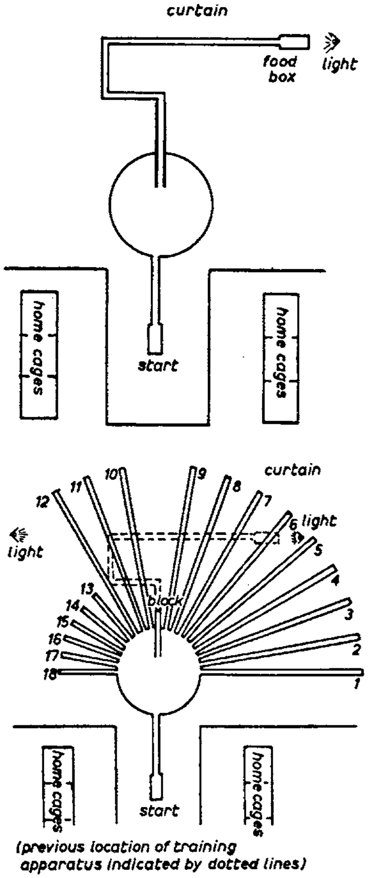


Figure 67. Test for sense of direction. Above, plan of apparatus in which rats are trained to make their way to food by an indirect route. Below, apparatus in which they are subsequently given the opportunity to go directly toward the original goal (along path 6). (After Birch & Korn [97], based on the design of Tolman, Ritchie & Kalish.)

8.2.3 Generalizing and Discriminating

Usually, when a rat is said to respond to an object in some specific way, such as jumping, it is implied that the object is always the same. But, as we saw in the brief discussion of stimulus generalization above, this is not justified. If animals responded only to external changes as narrowly defined as, say, the radio impulses which make a guided missile alter course, they would be hopelessly inefficient. In fact they respond to *populations* of stimuli; each population has a mean value for each of the measurable attributes of its members, and some variation about the mean. The variation depends (i) on the objects or processes which provide the stimulation, (ii) on the distance and direction of the source of stimulation, (iii) on the animal itself.

As for the first, if the objects responded to are other animals, they will certainly vary. The second source of variation is equally obvious: the angle or distance at which an object is seen, and the distance of the source of a sound, must influence the number and arrangement of the individual receptors (rods and cones, cells of the organ of Corti and so on) which are activated. The variation of this sort that can be tolerated may be considerable.

The third source of variation is the animal itself. Consider, with Osgood [514], an experiment in which a rat is standing on a grid, a tone of 1000 Hz is sounded and the grid is then electrified. The rat jumps. When training has made the rat jump at the sound alone, a tone of 900 Hz is presented instead. A less vigorous jump follows. With further lowering of pitch the intensity of the response declines further; at 500 Hz the rat merely tenses and quivers. A similar effect is produced if the pitch is raised. This is a simple, neatly quantitative, example of generalization.

The opposite process is discrimination. It is possible to train a mammal to respond to a narrow range of frequencies and to ignore tones outside that range. Such discrimination may be brought about experimentally in two ways. First, an animal may learn to respond to one stimulus, S_1, but not to another, S_2, measurably different from S_1, because response to S_1 is rewarded and response to S_2 is not. This is a case of conditional inhibition, such as was originally studied by Pavlov. Secondly, response to S_2 may be *punished*: S_2 will then come to evoke a response, namely, avoidance, which is incompatible with that produced by S_2. (The effects of punishment are further described in § 8.3.3.2 below.)

In the simplest type of discrimination, an animal is rewarded for responding to S_1, while responding to S_2 yields nothing. Much greater complexities are possible: (i) the alternative acts may both be rewarded, but to a different extent; (ii) the frequency of reward for alternative acts may be different; (iii) an animal may be required to reverse a discrimination.

Clayton used a **T**-maze to examine the effects of size of reward. On one side he offered one, two or four pellets of food, on the other, none, one or two; all possible combinations of these were used. Whenever the incentives were unequal, his rats eventually learned to go to the side where they received the larger reward [159]. A more interesting situation, for which again a maze with a single choice point may be used, offers different frequencies of reward on the two sides of the apparatus: on, say, 70 percent of runs there is reward on the left, on 30 percent it is on the right. In principle, two "solutions" to this problem might result. First, the probability of the animal's turning left might eventually stabilize at 70 percent—"matching"; second, there is the better strategy of "maximizing"—going always to the more frequently rewarded alternative. N. J. Mackintosh [423] has reviewed the evidence. Despite early reports to the contrary, rats trained on a 70:30 ratio tend to maximize: after long training they choose the more promising alternative on more than 95 percent of trials. Calfee has used an interesting experimental variant and has confirmed this finding. His rats were offered two possibilities. If they chose the correct one, they were given a food pellet in their home cage; if they chose wrong, they had to go to another goal box to get a pellet. When the ratios of reward were 80:20 or 65:35, most rats tended to maximize. When they were given 50:50, either they tended to alternate, or they developed a "position bias"—a tendency to visit one side of the apparatus persistently [122].

The most difficult discrimination problem commonly used experimentally requires an animal to reverse a recently acquired choice: the subject has learned to approach A and to ignore B; then, abruptly, approach to B is rewarded and approach to A is made fruitless. The acquisition of one habit might interfere with development of another, incompatible with the first. Ants (Hymenoptera, Formicoidea), set to learn their way through mazes, do display just this type of interference [708]; but rats, on the contrary, improve with practice. This is shown in serial reversal experiments (reviewed by N. J. Mackintosh [423]). The subjects are required to develop a spatial habit, such as going left rather than right, or a visual habit, such as discriminating white from black. When they have achieved some criterion, such as ten successive trials without error, the situation is reversed. Reversals are thereafter continued for as long as the experimenter's plan requires, or his tenacity allows. In one set of experiments, after eight reversals rats were making an average of only two errors on each reversal.

A further complexity of the discrimination process concerns the learning of difficult discriminations, such as that presented by similar shades of grey. If rats are to be trained on such a task, should they be started at once on the difficult problem? The common sense answer is to begin with something easier. As Lawrence has shown, on this question common sense is right: rats learned a difficult discrimination more readily if they were first trained on an easy one; and they were more efficient still if they were brought to the difficult problem through a series of progressive difficulty [399]. This finding is not at first surprising, yet it raises an awkward question: How do we account for a more ready learning of one discrimination as a result of acquiring a different one?

This question becomes still more pressing when we consider an effect of over-training. As described above, discrimination training is usually to a criterion of a short run of trials without error. Capaldi & Stevenson [138], N. J. Mackintosh [422] and others have studied behavior after more prolonged training. Common sense suggests that the longer the training, the less easy the reversal: an over-trained animal may be supposed to have developed the initial habit so well that it would strenuously resist discarding it. In this case, common sense is wrong: over-training leads to a more rapid learning of the reverse discrimination.

The attempt to explain this anomaly illustrates the present unfledged state of learning theory. The most promising suggestion invokes the existence of two processes underlying the altered behavior. N. J. Mackintosh, in his review, expresses this hypothesis in terms of "attention": "Animals must learn to attend to the relevant dimension as well as learning which value of that dimension is rewarded" [423]. Another formulation is that an animal learns, not only (i) to *approach* a specific stimulus (say, black rather than white), but also (ii) to *distinguish* between the relevant stimuli (and to ignore other features of the situation). On this basis, as Sutherland [659] has shown, an elaborate system of models may be constructed. Such a system may be discussed in terms of the overt behavior to which it refers. S. Siegel—who does not accept that the over-training reversal effect is explicable in this way—has reviewed the behavioral aspects of the subject [612]. But such a model is in effect a hypothesis about the central nervous processes which underlie the behavior. Eventually it, or a better one, must be tested physiologically.

When progress is made on these lines, it will have vast implications. Generalization and discriminations are necessary features of all complex habit formation. The precision with which an anamal adapts its behavior to complex situations must depend largely on these two processes. Moreover, generalization of shapes, that is, response to certain relationships shared by a number of patterns, may be taken as an index of "intelligence" (compare § 7.3.4.1). This is illustrated in figure 68: Fields and his colleagues (cited by Hebb) studied learning to respond to a series of triangular figures. Perhaps, for a rat, this process involves cerebral activities different from those of a chimpanzee (*Pan*); and the latter differs in turn from a young child.

What would ordinarily be called "intelligence" obviously depends on discrimination too. If an animal is presented, over a period, with a great number of rather similar stimuli, of which only a minority are accompanied by reward, and if that minority have only one feature in common which is not present in others, then the animal is faced with a difficult problem of discrimination. The capacity to solve such problems has been used to compare widely different species. One finding has been that fish lack the ability shown by rats in reversing discriminations. This and many other aspects of the experimental analysis of discrimination are reviewed in a symposium edited by Gilbert & Sutherland [260].

8.2.4 Social Stimuli

8.2.4.1 *Pheromones as cues.* In experiments on discrimination, visual stimuli are usually preferred by experimenters; but rats, as we know, are macrosmatic and readily discriminate odors. Among the odors to which they respond are pheromones (§ 5.2.3). It has been hypothesized that the pheromones secreted by wild rats change with their social circumstances, for example, when they are attacking or are attacked by a conspecific [52]. There is now at least evidence for secretion of "alarm" pheromones [144, 691]. Moreover, there is stronger evidence for a change in odorous secretions in relation to finding, or failing to find, food. The odors can evidently be discriminated, and may guide other rats in their choice of pathway. R. P. Morrison & Ludvigson, in one of a series of studies, tested this in a **T**-maze. Some of their rats were required to turn one way if the starting point smelled of rewarded rat, the other way if it smelled of unrewarded rat. The odors were laid by putting a rat in the **T**-maze, and giving it either food or an empty food container. Training in this and other, similar discriminations was successful [480].

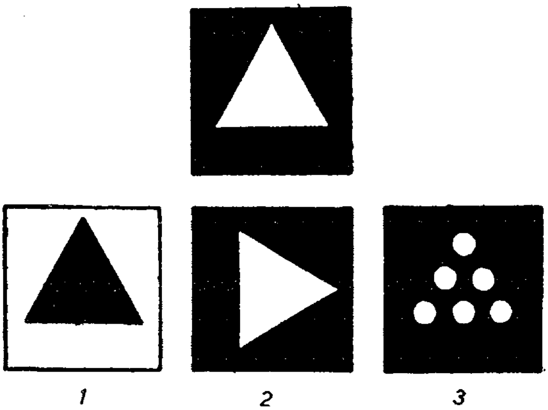


Figure 68. A test of "intelligent" behavior. A rat trained to respond to the top diagram makes random responses to any of the others. A chimpanzee (*Pan*) responds to diagrams 1 and 2. A child (*Homo*) of two years recognizes all three of the lower diagrams as triangles. (After Hebb [in 554].)

Further experiments, by Seago and others, confirmed that this behavior depended on olfactory stimuli: anosmic rats failed to make the discriminations. As these and other authors point out, such findings are important for the design of experiments. For many investigations, stringent cleanliness of the apparatus may be crucial [452, 595, 649]. Now that this field has been opened up, further progress seems likely to be rapid.

8.2.4.2 *Following and imitation.* We now turn to the most complex social influences on habit formation: in ordinary speech, these are said to involve imitation and even teaching in some sense. In § 4.3.3 we saw something of the difficulties of distinguishing imitation from mere following. Rats were readily trained to follow another rat, but the leading rat was merely a cue: there was no true imitation. Angermeier and others give another example. First, rats were trained to escape electric shock by leaving a box when a buzzer was sounded. These were "demonstrator" rats. When they had been trained, two were put in the shuttle box with each experimental rat, and the buzzer was sounded. The trained rats duly moved into the other compartment. After a series of trials, some of the experimental rats also developed the habit of "escaping" at the sound of the buzzer, although they had never received shock. This habit was retained even when they were put in the apparatus alone. A control group did not develop the habit [20]. In this case, although there was much individual variation, some of the experimental rats evidently developed a habit of following the other rats; and this behavior came, by contiguity, to be evoked by the buzzer alone. Hence their behavior was *as if* they had learned from the trained rats that the buzzer signaled danger; but in fact there was no evidence that the behavior of the followers was determined by the shock experienced by the trained rats: the followers were simply influenced by the movements of the trained rats.

It is now necessary to state as precisely as possible what is meant by imitation in a strict sense. A definition modified from one by Thorpe [676] is: the copying of a novel or otherwise improbable act. The act must not be one which would be likely even in the absence of an exemplar. Imitation in this sense may also be called "learning by observation"; this indicates the type of experiment needed to test for imitation. A teacher, or demonstrator, D, is trained to perform a complex pattern of movements: for instance, it is required to pull a string and so to get access to a tray bearing food. D is in a cage separated by a glass partition from another containing the pupil or observer, O. No reward is given to O during its periods of observation. The question is whether O stores any useful information while watching D. This is tested by setting O the same problem when its periods of observation have been completed. Domestic cats can benefit in this way: a recent example is given by John and others [348].

Until recently there was no convincing evidence that rodents can learn by observation, but now some has been provided by Zentall & Levine. They trained laboratory rats to press a bar for water in a Skinner box from which another box could be seen. The second box contained one of the following: (a) a rat drinking; (b) a rat pressing the bar; (c) nothing; (d) a rat ("naïve") doing nothing relevant. Of these four groups, the rats that could see the bar being pressed developed a higher rate of bar-pressing than the others. Those that saw a naïve rat developed the habit less readily than the rest. The last finding is perhaps attributable to distraction. Hence there is some reason to believe that even laboratory rats can imitate [737].

Imitation is a property of the pupil, and has been much studied [465]. The other side of the coin, teaching, has been oddly neglected by students of behavior. Ewer [228] gives examples of parental *encouragement* of the young: this is important among carnivores; it consists of behaving so that the young have the opportunity to develop new habits, such as those involved in food-getting. But the concept of teaching includes more than this: the teacher must not only induce a specific change in the behavior of another individual, but must also persist in the relevant behavior, and adapt it, until the pupil achieves a certain standard of performance [44]. In this sense, there is only one type of situation in which teaching is observed generally among mammals, namely, where punishment is used to induce withdrawal of an animal from a conspecific. It occurs when young are being weaned, juveniles or subordinates are being driven away, and intruders on a territory are driven out. The use of punishment to engender new and complex habits seems to be confined to man.

8.3 REWARD AND PUNISHMENT

8.3.1 What is "Reward"?

8.3.1.1 *Definitions.* Generalization and discrimination ensure that an animal responds to an appropriate range of objects in a given class. We now consider further what determines whether an animal responds at all. As we know, response to a given situation depends on internal state. If an experimenter wishes an animal to perform an act, he usually arranges that the performance is followed by satisfaction (if only partial) of a bodily need (figure 69). Typically, he deprives the animal appropriately beforehand. We must now say something more precise and detailed about reward, or reinforcement, and its relationship to performance. The subject has been extensively reviewed by Kimble [364] and by Bolles [100].

A reward or positive reinforcer may be defined as a stimulus which increases the strength of a response which evokes the stimulus. This definition obliges us to consider the meaning of "habit strength": how do we represent the progress of habit formation against time or against exposures to the relevant situation? Pavlov, in his most celebrated experiments, used the amount of saliva secreted on successive presentations of a conditional stimulus. This is an example of the *amplitude* of the response. A second measure is the *frequency* of responding, as recorded in, for example, a Skinner box (§ 7.2.1.3). A third is *latency*, that is, the interval between application of a conditional stimulus (or situation) and performance of the act; this, or a reciprocal measure (the *speed*), is easily used in a maze experiment. Fourth, and finally, is *resistance to extinction* (§ 8.5). Unfortunately, these criteria are not always highly correlated, as we shall see. Hence, one should always specify the feature that has been measured.

8.3.1.2 *Quantity.* We now turn to the relationship of reinforcement with the various measures of response strength. An obvious likelihood is a quantitative one: the greater the reinforcement, the greater or quicker the response. Spence has summarized relevant experiments by Sheffield and others. They recorded speed of running along a passage as a function of the sweetness, nutritional value and previous opportunity of drinking a solution of saccharin (sweet) or of dextrose (nutritious but not sweet); they also measured the rate of consumption of the solution. There was a precise relationship between response speed and amount drunk, that is, the amount of consummatory response performed. In another study a similar relationship was found when the reward was the opportunity to copulate: speed was correlated with the vigor of the copulatory activity [635]. P. T. Young & Shuford studied the reinforcing effect of sucrose solutions of various concentrations; the criterion was again the speed with which rats approached the solution, but in their experiments the rats were sated, not fasted: speed was a function both of sucrose concentration and of length of time during which the rats were allowed to drink [731]. Guttman used a different response: he trained rats to press a bar for sucrose solution. Once trained, the rats were tested with different concentrations of sucrose but allowed only the same amount of drinking. The rate at which the rats pressed the bar rose with concentration until 32 percent sucrose was offered, when there was a decline [277]. Kraeling recorded both the speed of running in an alley and also the number of licks with the tongue (or consummatory responses) in relation to the strength of sucrose solution: again, solution strength proved to be a crucial factor in the amount of consummatory response [378].

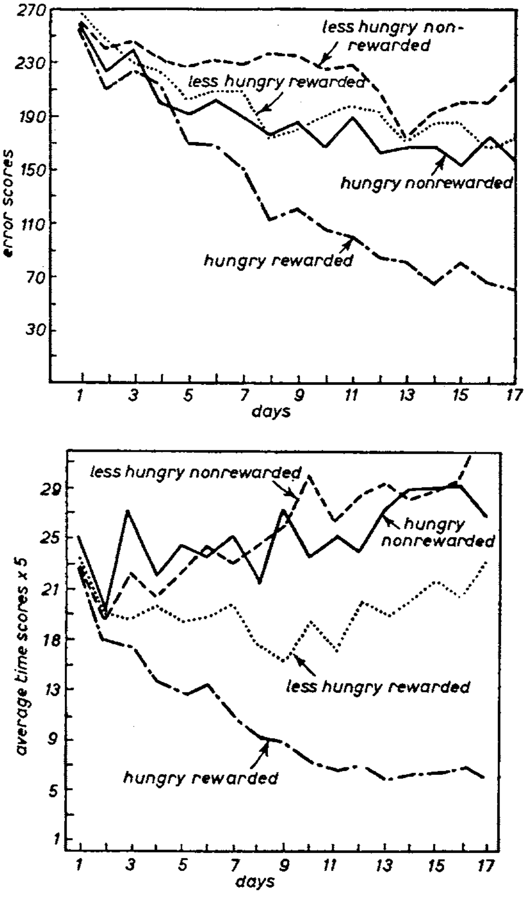


Figure 69. Effect of reward on habit formation. Time taken in a maze and number of errors made decline steeply with training only if the animals are both "motivated" (fasted, in this case) and appropriately rewarded (with food). (After Tolman & Honzik [683].)

8.3.1.3. *Change of quantity.* In most experiments involving reinforcement, the amount of reward presented on performance of the rewarded act is constant. What happens if, after training, it is altered? Crespi recorded the running speed of rats in a straight runway after a fast of twenty-two hours. The amount of food at the end of the runway was varied. If rats which had been trained on one or four units of food were given sixteen units, their running speed went *above* that of rats trained throughout on sixteen units. Correspondingly, rats trained on 256 or 64 units, and shifted to sixteen, came to run at a speed *below* that of the sixteen-unit group (figure 70). These observations are most readily (and most usually) described in anthropomorphic terms, namely, "elation" and "disappointment" [180]. They have been fully confirmed. As an example, Dufort & Kimble trained rats to run an alley to a 10 percent glucose solution. When trained some of the rats continued to be run to a 10 percent solution: these maintained a steady running speed, but continued to improve in the proportion of correct responses they made. Rats given a 5 percent solution after training declined in both respects; others, given 20 percent glucose, markedly improved, especially in running speed [210]. Such experiments (and others, cited by Bolles [100]) imply that there are processes in the brains of rats which, on the basis of previous experience, anticipate the consequences of action (§ 8.4). Yet a further example, in which a change of quality is involved, is given in figure 71.

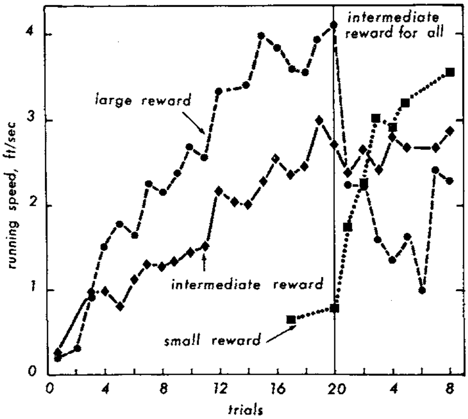


Figure 70. Elation and disappointment. During the first twenty trials, rats were run for high, medium or small rewards; after that, they were all run for medium reward. (After Crespi [180].)

8.3.1.4 *Frequency.* In most of the experiments described above, each correct response was rewarded. Skinner made a series of studies of "partial reinforcement" [235, 613]. He used, of course, the Skinner box. One method is to give the reward only once in a given percentage of correct responses (figure 72). This itself can be done in two ways. First, the intervals may be regular: for instance, every tenth response may be rewarded. In this case the response rate of a trained animal slows down just after reward but speeds up again just before the next reward is due: this is evidence, once again, of anticipation of the reward. Second, the intervals between rewards may be irregular and unpredictable, even though, over a long run, the proportion of rewarded responses is still 10 percent; the response rate is then steady and is little affected by reward when it comes.

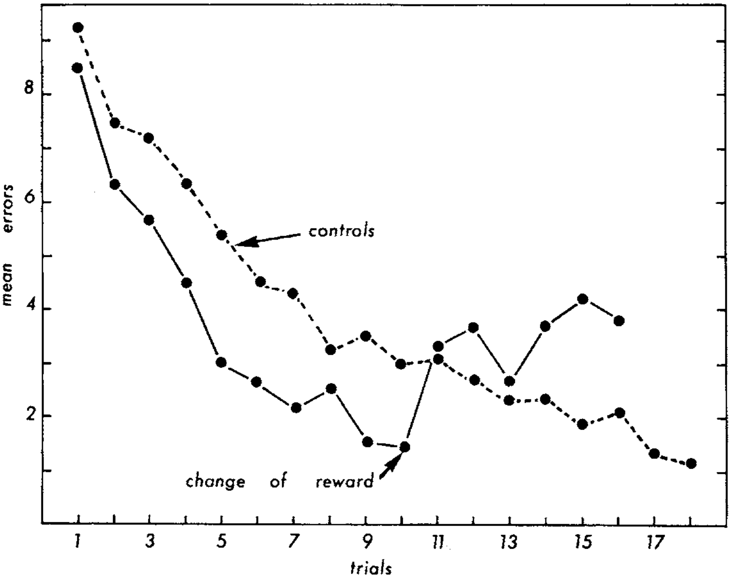


Figure 71. Change of reward. Habit formation in a maze recorded by the decline in number of errors with time. After day 9, the experimental group was rewarded with sunflower seeds instead of the wet mash they had previously received. Their error rate then rose even above that of controls which had received the seeds throughout. (After Elliott [215].)

When the application of reward is determined by *number* of responses made, lowering the incidence of reward increases response rate: giving a food pellet once in a hundred responses produces a higher response rate than giving it once in ten. But another way of applying partial reinforcement is to space out the rewards by time, regardless of response rate. This has a different kind of effect: if the reward is given once per hour, the response rate is lower than when the reward is given ten times per hour.

These observations are not very surprising, though they could conceivably have some practical applications. Of more interest is the observation, made by Mowrer & Jones [487] among others, that 50 percent reinforcement can give as rapid habit formation as reinforcement of every correct response. The significance of this is obscure. Further, the effects of different sorts of partial reinforcement on response rate during training (and hence on learning) are not the same as their effects on extinction. Habit formation is faster when a high proportion of responses is rewarded. But, by contrast, *extinction* occurs more quickly when the incidence of reward is higher (figure 73). In other words, when reward is withdrawn, a habit is only slowly lost if the animal has been accustomed to being rewarded only seldom. This is a neat example of the need to specify just what feature of response strength one is using as a criterion, either in a given set of experiments or in drawing conclusions. It also illustrates the fact that even one of the conventional categories of "learning" covers a number of processes imperfectly correlated with each other.

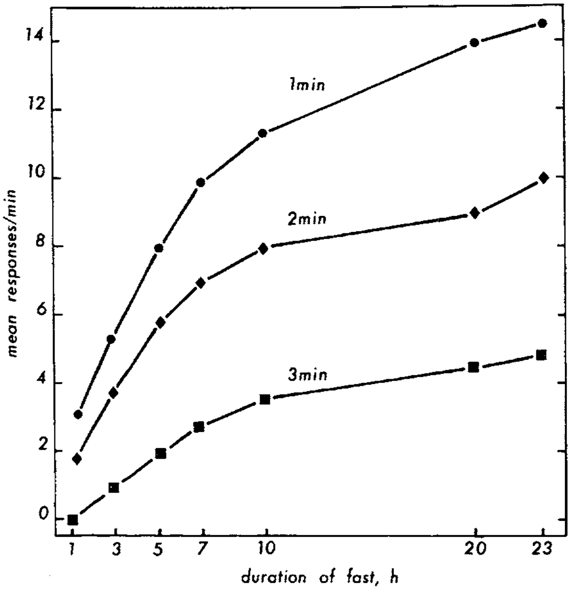


Figure 72. Effects of incidence of reinforcement and length of fast on rate of bar-pressing in Skinner box. For all rats, the interval between rewards varied at random; but for one group the mean interval was 1 min (upper curve), for a second group, 2 min, and for a third, 3 min (bottom curve). (After Clark [157].)

8.3.1.5 *Delay.* In most experiments on habit formation, the reward is presented, after performance of the required act, with as much promptness as the structure of the equipment allows. But a rat can learn *not* to respond by bar-pressing during a delay before the reward is delivered. To achieve this, the animal should first be trained on simpler schedules with no delay. We now consider what happens if reward is delayed, but without any complication such as requiring the animal to stop responding. Grice gave rats the easy problem of discriminating between black and white, but sometimes allowed them their reward only after an interval. This led to severe impairment in acquisition of the habit: a delay even of ten seconds completely prevented some of the rats from developing the habit [270]. This is one of many such findings.

Nevertheless, in some conditions rats can overcome the obstacle of delay. This is obviously true when a maze with many choice points is mastered.

Bolles, in a critical analysis [100], discusses the paradox that these findings present. Some observations imply that reward must be immediate if it is to induce habit formation; yet others seem to contradict this. One attempt at explanation invokes secondary reinforcement, defined as a reward or reinforcer whose effects are acquired through association with another reward. Examples are given below (§ 8.3.1.6). On this view, features of the experimental situation, other than the primary reward, come to function as rewards.

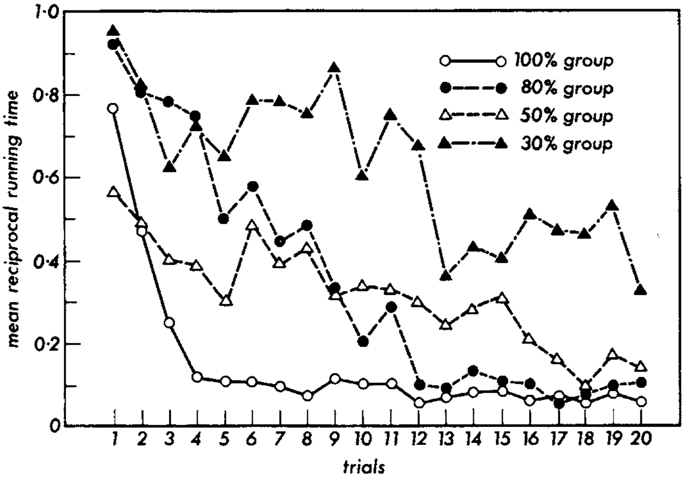


Figure 73. Extinction. The curves show the rates at which a running response was lost by rats which had experienced different incidences of reward during training. Those rewarded on each trial had the highest extinction rate, while those rewarded least often (on only 30 percent of runs) lost the habit least quickly. (After Weinstock [706].)

Supporting evidence comes from studies of extinction of habits acquired despite delay of the reward. Sgro & Weinstock, among others, have observed slower extinction in these conditions than when the reward is immediate. The rats in their experiments were required to run for a reward. On this hypothesis when, to test for extinction, the reward is withdrawn, the associated conditions of the runway continue to have a rewarding effect [600].

A few experimenters have taken a wider view of the effect of delay. Logan used a maze consisting of two parallel alleys with a common starting point. His maze allowed him to delay an animal in either runway for a chosen period. He varied not only the delay, in the two runways, but also the amount of food offered as reward. As expected, the animals showed a preference for the larger food reward; and they also preferred a brief delay to a longer one. The most notable finding was that they preferred no reward at all to a small reward reached only after a delay [417]. Hence delay is, in this situation, aversive. It does not, however, lead to any general disturbance of behavior. As Wist has shown, an animal delayed during a sequence of activities displays the effect only in performing that part of the sequence which comes just before the delay [718].

These effects of delaying reward suggest two comments. First, every additional batch of ingenious experiments on habit formation adds a new complexity to the total picture. A unified account of the subject is not in sight. The second concerns the biology of the animals studied. Despite the status of rats as mammals with—in relation to the whole animal kingdom—quite large brains, there is nothing in the behavior reported which can be called foresight. If experiments of the kind described above are "intelligence" tests, the laboratory rat is intellectually a poor performer.

When, however, we turn to effects of aversive stimuli, we find rats capable of notable achievements. In § 4.3.1.2 experiments are described in which "learned associations over long delays" were observed as a result of ingestion of sub-lethal doses of poisons. The phrase quoted is from a review by Revusky & Garcia [541], in which these and related findings are discussed in relation to conventional views of habit formation and memory.

As an example, laboratory rats are allowed to drink an unfamiliar mixture, such as water flavored with sucrose; then, after 6.5 h, they are irradiated sufficiently to cause illness but not death. On subsequent testing, the animals reject the sweet solution. We have here, then, an "aversion due to ingestion-contingent toxicosis" which has developed despite the long interval between the two relevant events. A number of other mammalian species have the same ability; and the aversions can be to a great variety of liquids and solids.

These aversions are to flavors. It has not been found possible to relate an external stimulus to toxicosis in the same way. This has led to the concept of "stimulus relevance": an animal readily learns to associate toxicosis with a flavor, even when a delay of some hours is involved, but not with a stimulus such as a noise or a light. The significance for survival is obvious, but the physiology involved remains to be found out.

8.3.1.6 *Secondary reward.* A further question bearing on the "intelligence" of laboratory rats concerns their ability to respond to stimuli which are not primary rewards. Demonstrating this capacity unequivocally in rat behavior has not been easy [100, 364]. Some of the difficulties are illustrated by Wyckoff and Miers. Rats were trained to approach and lick a water source in response to the sound of a buzzer. Next, the water—that is, the reward—was withdrawn. The rats were then tested to see whether they would learn to press a bar in order merely to hear the buzzer. The object was to determine whether the sound had come to act as a reward. The rats did in fact quickly learn to do this, and so it seemed that here was a case of secondary reward. A control group was, however, given the task of learning to press a bar when the only reward was that of turning the buzzer off. These rats, too, developed the bar-pressing habit, just as readily as the experimental group [726]. In this case, what was observed was evidently an example of the reward value of an alteration of the environment (already discussed in § 3.2.4).

The standard successful demonstration of secondary reward is that reported by Saltzmann. In his well-designed, careful work, the crucial question was this: if rats had previously experienced reward (food) in a particular type of goal-box, would they show a preference for this box (even when empty) over another? All the rats were trained to run a straight alley for food offered in a distinctive box. They were then run in a maze, with a single choice point but without food on either side; on one side there was a box in which they had previously experienced food; on the other, there was either a completely strange goal-box, or one in which they had experienced an absence of reward. The second box was sharply distinct from the reward box (black instead of white, or white instead of black). In the second case especially, there was a decisive preference for the box in which food had been experienced [574].

8.3.2 Abolition of Deficit

Evidently, only tentative general statements are possible about the relation of reinforcement to response strength. We now turn to the related question of the influence of internal state on habit formation. In experimental studies, a reward is usually something which tends to make up an internal deficit. Hence we have the notion, associated especially with C. L. Hull [339], that reinforcement depends on drive reduction. This, sometimes called "the law of effect" from an earlier version proposed by E. L. Thorndike (1874–1949), has a basis in some obvious facts of physiology: many features of the animal body are maintained in a steady state; for this to be achieved, the external conditions, such as temperature, must remain within a certain range, and certain substances must be available. Departure of any of these from a certain range of values is said to set up a "drive state"; and reduction of this state is held to be the invariable accompaniment of reinforcement. Although, perhaps, nobody now holds this view in just this form, it is still instructive to consider the evidence which bears on it.

Some deficits, for instance of food, can increase activity (§ 3.2.1.2). During its movements under deficit (so-called appetitive behavior), an animal learns how to abolish the deficit, for instance by visiting a particular spot or by making some special movement. This achieved, the animal turns to another sort of activity or becomes quiescent. Hence "need reduction" seems to determine what habits an animal will develop. But, when detailed analysis is attempted, the relationship between internal state and overt behavior proves to be far from simple. We must therefore turn to experiments in which particular internal states, precisely defined, are varied, and the effects are observed on components—also accurately measured—of habit formation.

O'Kelly & Heyer studied maze-learning by rats deprived of water. Some had been without water for eleven hours; others, similarly deprived, had also received injections of sodium chloride to give—in osmotic terms—a "thirty-six-hour thirst": maze learning was the same for the two groups, even though the second group drank more water on each run. Here the *duration* of the period of need (11 hours in each case) evidently determined the speed with which the habit (maze-running) was developed, but did not decide the intensity of the consummatory response (drinking) [506]. Efficiency of habit formation, then, is not always correlated with bodily deficit. Another example has been reported by Deese & Carpenter. Rats were trained to run a straight alley, about one meter in length, to food. Half were run just before receiving their daily meal, half after feeding. Both groups were given four runs a day for six days. Then the situation was reversed: the rats which had previously been run after a fast were put in the maze after feeding, and vice versa. The rats which had been trained when sated changed their speed of response immediately after the switch was made; that is, they came to behave like the other group during the first phase of the experiment. But those which had been trained under deficit did *not* lose their high rate of response when they were run after feeding [189].

An important question for experimentalists is how animals can be kept over many days in a steady state of responsiveness. Some workers assume that there is something, called a "drive state" perhaps, which with sufficient ingenuity can be held constant during a long series of observations. In its crudest form, this amounts to saying that, since there is a name ("drive-state") there must be something identifiable in the animal corresponding to it. But, of course, the existence of a word never proves the existence of a veridical class of events. The proper procedure is (to repeat) to identify measurable internal features which can be shown to influence behavior.

The optimum internal deficit for a given performance must, then, be determined for each type of situation; but there are some general rules. One is that the optimum deficit tends to decline as the difficulty of the task is raised. This, the Yerkes-Dodson law, first formulated in 1908, has been tested by Broadhurst. He gave rats a brightness discrimination which had to be made under water; the discrimination was made easy, medium or difficult. Four levels of deficit were contrived, by keeping the rats submerged in water for eight, four, two or no seconds before releasing them to swim through a T-maze. A correct choice enabled them to come to the surface and breathe. Figure 74 shows that for learning the difficult discrimination there was a marked optimum at two seconds of deprivation of air.

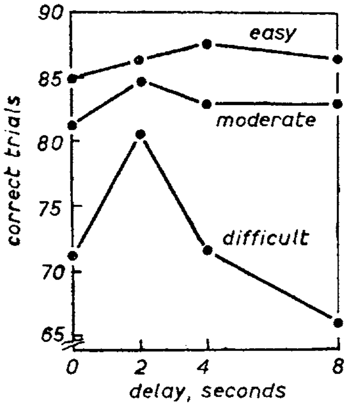


Figure 74. Effect of severity of discomfort in relation to difficulty of task to be learnt. Given a difficult brightness discrimination (bottom graph) rats performed best when held only two seconds under water before being allowed to swim on their own. (After Broadhurst [107].)

Broadhurst's experiments used a deficit of oxygen. Two examples illustrate how the precise character of a food deficit may be investigated. Collier with others has described experiments on the rate of bar-pressing for food or water in relation to deficits. Pressing the bar yielded a reward of sucrose solution. The experimental animals were kept on a diet so restricted that they lost weight. The amount of nitrogen present in each ration was kept constant. Earlier studies had shown a relationship between a reduction in body weight and readiness to press a bar for food. Collier and his colleagues established a precise relationship: the log rate of bar-pressing was exactly proportional to the log loss of body weight. An unusual feature of this work was that these workers were not content merely to record changes of weight, but also made estimates of chemical changes which accompanied it. The proportion of DNA in the liver rose, and correspondingly the ratios of RNA and of protein to DNA declined with the decrease in calorie intake. The cells of the livers which displayed these changes were smaller, and hence more numerous per unit weight of tissue. These authors suggest that the primary stimulus for extra eating after loss of weight should be sought at the cellular level [166]. In an accompanying study, Collier & Levitsky induced a decline in body weight by reducing the amount of water available, and hence the amount of food eaten. Their findings supported those described above [165].

The internal adjustments which accompany a change in behavior, such as an increase in food consumption, are obviously many. A simple assumption is that, if an animal is deprived of food or water, there will be a proportional increase or decrease in the bodily states affected, at least until the animal is grossly weakened. Similarly, it might be assumed that the readiness with which an animal would learn to get food would be proportional to the length of fast or some other simple measure of deficit. We have, however, already seen that, on the contrary, there is an optimum deficit for efficient performance. Bélanger & Feldman have expressed this notion in terms of "drive": is the "level of instrumental response" proportional to "drive" (that is, the deficit or degree of deprivation)? They used the heart rate as an index of level of arousal or of autonomic activity (or "drive"). Their object was to test proposals by earlier workers that the relation between "motivation" and certain features of performance is an inverted **U** (figure 23). During seventy-two hours without water, heart rate rose steadily (figure 75). The rats were in a Skinner box, and their rate of bar-pressing for water was also recorded. This rose at first, like heart rate, but later declined. The immediate conclusion is that, if one wishes to train a rat in some habit, with water as the reward, the best level of deprivation is substantially less than the maximum a rat can survive [81]. Other relevant findings and hypotheses have been reviewed by Malmo [432] and by Malmo & Bélanger [433].

Unfortunately, some further experiments, reviewed by Campbell & Misanin [131], have failed to confirm the rather simple relationship originally proposed. Among them are the findings of Collier and his colleagues, described above: on the "inverted-**U**" hypothesis, they should have found a decline in performance by their rats at the most severe levels of deprivation; but they did not. Accordingly, "this concept is at a stage of crisis" [131]. Hence it resembles a number of attractive theories on the physiological basis of habit formation.

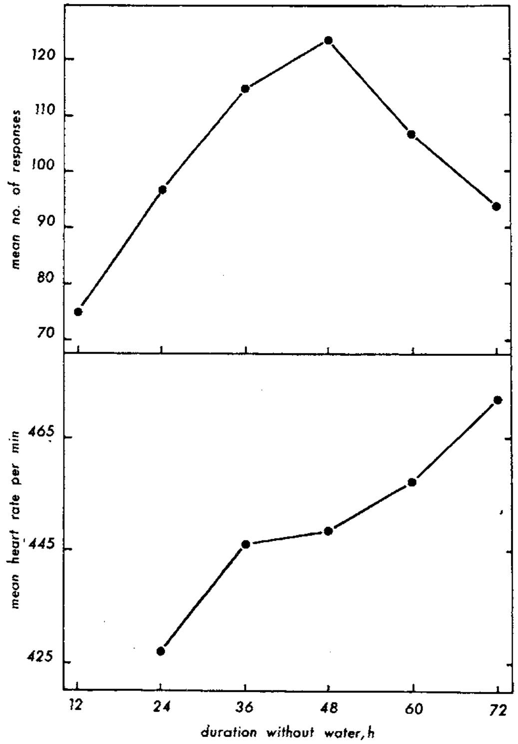


Figure 75. Rate of bar-pressing for water is maximal after 48 h deprivation (upper curve), but heart rate during responding continues to increase over 72 h (lower curve). (After Bélanger & Feldman [81].)

So far this section has dealt only with behavior which contributes directly to homeostasis. Even when we confine ourselves in this way, we see only a complicated set of relationships between internal state and behavior. But habit formation can also be induced by rewards of a different sort. The opportunity to move around, or to watch moving objects, has this property (§ 3.2.4). For satisfying immediate homeostatic needs, such acts are waste of time: they certainly cannot be related to any internal deficit. Though exploratory learning contributes indirectly to survival, at the time at which it occurs the activity involved merely depletes the animal's energy resources. It might be argued that there is an "exploratory drive" which is reduced by exploration. But such an argument becomes no more than a tautology: an act is said to be performed only because it leads to drive reduction; and when we ask how we know that drive reduction has occurred, the only answer is that it must have occurred—because the act was performed.

There are also many examples of reward value in activities which, by themselves, are of no biological use. An example is the performance of coitus without ejaculation. As we saw in § 6.1.1, male rats have to copulate a number of times before they ejaculate. Sheffield and others have shown that the opportunity to copulate without ejaculation can lead to the development of a habit (figure 76).

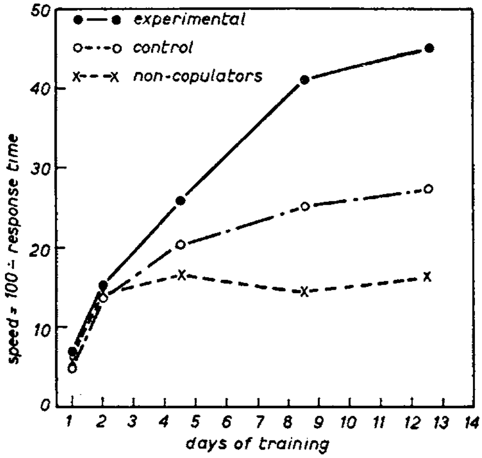


Figure 76. Reward value of coitus without ejaculation. The experimental animals found a female in the goal box of a maze; they performed coitus but were removed before they reached the stage of ejaculation. Control animals found a male. The bottom graph refers to animals which did not attempt coitus, whether they found a female or a male. (After Sheffield, Wulff & Backer [605].)

In the form in which it is sometimes stated, the theory of drive reduction is a misapplication of a biological principle. One may suppose that every feature of an organism is a product of natural selection; and that it has, or has had, survival value. (Some features of organisms may be *indirect* consequences of processes with survival value.) But it does not follow that all behavior directly and immediately contributes to homeostasis. For mating and the care of young, this is a truism, but it applies even to behavior related to ingestion. Rats display preferences for substances, such as saccharin, which are not related to their nutritional value (§ 4.3.2). They can, sometimes, adjust their intake according to need, especially for energy, but they are not infallible. This is to be expected. Natural selection so operates that the behavior of an animal, *in the conditions in which its ancestors have survived,* conduces to survival of the species; but the means by which this is achieved are diverse and may be indirect. (This, of course, by no means precludes survival also in novel environments. *Rattus norvegicus*, for instance, is obviously to some extent pre-adapted for life in laboratories.) When an animal is subjected to quite bizarre conditions, its behavior is likely to be bizarre too, and to fail to relate response to need. This is outstandingly the case in the experiments, described in § 2.4, on self-stimulation. Although an animal's behavior reflects the action of natural selection, just how the behavior is related to survival must be investigated in each particular case. It cannot be determined *a priori*. Accordingly, what constitutes an inducement to develop a habit may have anything from a direct to a very tenuous relationship with survival.

8.3.3 Training in Avoidance

8.3.3.1. *Aversive stimuli.* Despite the conclusion of the last paragraph, much habit formation is related straightforwardly to obvious bodily needs. The needs referred to in the preceding sections have been mainly those that can be satisfied by *approaching* a source of stimulus. But there are others that demand flight. To put the point in another way: there are events outside the animal of which the *removal* increases response strength. We now, therefore, examine aversive stimuli, and the experimental conditions in which their effects are studied. The subject is reviewed in a symposium edited by Campbell & Church [130].

An aversive (or noxious) stimulus is one which tends to induce withdrawal (escape) or avoidance. The two effects are distinct (figure 77). If an animal is shocked in a shuttle box (§ 7.2.1.4) it at first *escapes* after the shock has come on; but, if the onset of shock is signaled in advance, it learns to *avoid* the shock by responding to the signal or conditional stimulus (CS). An aversive stimulus may similarly be used in a Skinner box, in which escape or avoidance depend on pressing the lever.

The choice of aversive stimulus by experimenters seems usually to have been determined by convenience, and not by biological significance: that is, the sorts of aversive stimuli that an animal is likely to encounter in natural conditions have not been considered. Electric shock is widely used for several reasons: (i) it is exactly reproducible; (ii) it is easily varied quantitatively; (iii) if it is applied to a rat's feet, an experimenter can be confident that it will reach its target. Nevertheless, there are some complications. Rats can sometimes learn to adopt a posture which reduces its effects [100, page 180]; and, as Coons and others have shown, rats may become rapidly less responsive or even indifferent to shock after a few applications [169]. Coons and his colleagues used a Skinner box in which shock was applied to the floor grid and could be turned off by rotating a wheel. N. E. Miller independently made a similar observation on rats trained to run an alley for food. The trained rats were given gradually increased intensity of shock at the goal point, and became indifferent to this stimulus. Miller describes the change as "learning resistance to pain and fear" [462], but the question of what precise meaning may properly be given these terms must be deferred. R. K. Banks made a further study on the same lines: one group of rats was intermittently shocked during training to run an alley; this led at first to a delay in approaching the goal, but the delay had almost disappeared after nine trials. The experimental group, and a control group which had received no shocks, were then shocked on every one of a series of further runs: in these conditions the controls took much longer to reach the goal than the experimental group [35].

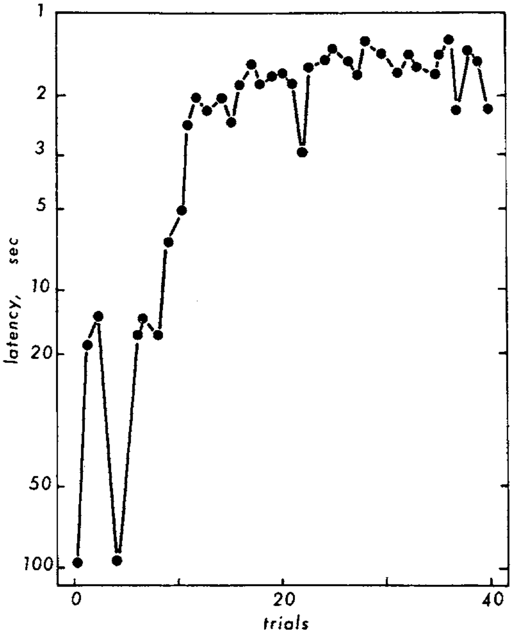


Figure 77. Escape followed by avoidance. A rat was shocked unless it moved from one part of a cage to another. On the first seven trials it escaped after being shocked; thereafter it avoided shock by moving when shock was signaled, before shock was switched on. The vertical axis gives the latency (delay before response) on a log scale. (After Solomon & Wynne [629].)

Habituation occurs only to shock of low intensity. There are examples, discussed by Bindra [94], of a tenacious resistance to extinction of an avoidance acquired after only a few experiences (occasionally only one) of severe shock.

Severe shock can have wider effects than the mere suppression of a single response. Estes trained rats to press a bar, then shocked them whenever they made this response. This unsurprisingly led to a loss of the bar-pressing behavior. But, as a control, he also administered shocks in the same apparatus, but independently of the response. The result was much the same, namely, a loss of the bar-pressing habit [224]. Similarly, Moyer & Korn found both escape and avoidance in a shuttle box to be disrupted by severe shock [488]. Church, in a review, accordingly refers to the "general emotionalizing effect of punishment" [156]. Such expressions make description more vivid, but do not identify the processes involved. Theios and others have, however, taken a step further: they confirmed the adverse effect of severe shock on behavior in the shuttle box, but they also tested its effect when the animals are required only to move one way to escape shock: that is, from side A to side B, but not—as in the usual type of experiment—also back from B to A. In the changed conditions, the higher intensity of shock had no adverse effect on the development of the habit. Hence, these authors attribute the effect of high shock on the normal shuttle box habit, not to a general disruption of behavior, but to slow extinction of the response of going from A to B when the animal ought to go from B to A [670]. This finding does not, of course, exclude the possibility of a general disruptive effect in other conditions.

Punishment is further discussed in the next section. We must now briefly consider other types of external aversive stimuli. These include a sharp puff of air in the face, abrupt exposure to extremes of heat and cold, immersion in water, and very bright light. Although it is possible to imagine any of these occurring in nature, none is probable. We therefore turn to noises, which are an important feature of the lives of wild rats in natural conditions. Campbell was able to train rats to perform a task by rewarding them with a reduction in the amount of noise to which they were subjected; the rate at which the habit developed was proportional to the degree of noise reduction [127]. Unfortunately, this is only an isolated observation. There is need for more information on what types of noise are most aversive, the circumstances in which they are most effective and the readiness with which habituation to them can develop.

Presumably, in natural conditions, one of the most important types of aversive stimulus is being seized by a predator. Something of this sort can be simulated in the laboratory by picking a rat up in one's hand. A wild rat so treated struggles, squeals and bites. Perhaps the violent behavior sometimes induced by electric shocks [688]—the so-called "shock-induced aggression"—is the laboratory rat's equivalent to an anti-predator response. (§5.4).

In view of the enormous numbers of laboratory rats which have been manipulated by experimenters, it is surprising that there is no great body of quantitative information on the effects of the mild treatment of handling. Sometimes, it is rewarding. Mahut [426] trained rats to run a straight alley, and then put them on an extinction schedule: that is, she ran them without reward. As expected, the rate of running diminished; but after a time, it rose again, as if the rats were once again being rewarded. In this case, evidently, they were: ordinarily these rats adopted the characteristic stiff posture when picked up, but those which had received regular handling relaxed when held. This observation has an obvious methodological significance: clearly, the effects of handling can interfere with the results of an experiment. Worse than this, Candland and his colleagues report an opposite effect. Their rats were each kept in a box with two compartments; when they were in one compartment, they were regularly picked up and stroked. As a result, they came to avoid that compartment [135]. In this case, handling was an aversive stimulus, as it would be for a wild rat.

Probably, handling is more often aversive than rewarding, but this perhaps depends in part on the strain of rat and the behavior of the experimenter. And Wong has described the effects of yet other factors. The laboratory rats he used were allowed to move between two compartments, differently painted; if, at a given moment, they were in the critical compartment, they were removed and stroked for twenty seconds. Some of the rats had been regularly handled in infancy, others not. The observations described above, and others cited by Wong, leave it doubtful whether this treatment would act as a reward or a punishment or neither. Most of the rats learned to avoid the critical compartment: that is, for them, handling was aversive, or constituted a punishment. But one group was exceptional: the females which had been handled in early life were unaffected, in their choice of compartments, by the handling. These observations, then, illustrate a disconcerting interaction between sex and early treatment, and show how conflicting findings can arise from well conducted experiments [722].

8.3.3.2 *Punishment.* The term "punishment" is conveniently defined as a response-contingent aversive stimulus: for punishment to occur, then, an animal must perform some clearly defined action. As we know, when an aversive stimulus is of mild intensity, the result is typically a weakening of the response. This weakening undergoes extinction if the training is not kept up [224]. An important feature of punishment, in which it differs from reward, is the restricted character of its effects. The development of a new habit is usually due to the combined effects of an internal deficit, ranging ("appetitive") movements, and a response-contingent reward that matches the deficit. But all punishment can do is diminish the performance of an existing response, or strengthen the habit of performing the behavior which the punishment elicited from the start: such behavior includes withdrawal, and the adoption of an immobile posture [100].

The way in which the effects of punishment are tied to pre-existing responses has been illustrated by Fowler & Miller. They trained rats to run an alley for food. When trained, some were shocked at the goal point on their forepaws, the others on their hindpaws. The first group were slowed down in their running by the shock, but the second group were speeded up. In ordinary conditions it is, of course, adaptive for a rat to run swiftly forward if its hind regions are hurt, but to withdraw in another direction if the injury is anterior; these responses were strengthened by the two treatments [241]. Hence, the response to punishment by a rat has no necessary, direct relationship to avoiding the aversive stimulus.

At the extremes of intensity of stimulation, there are further complexities. First, as we have seen, noxious stimulus of high intensity can have an adverse effect on behavior (§8.3.3.1). This is illustrated in work by Moyer & Korn (figure 78): in their experiments, shock intensity above a certain level reduced the percentage of successful avoidances, and increased delay before effective action was taken [488].

There are also some paradoxical effects of mild stimulation. The classical example is due to Muenzinger. He trained rats in a visual discrimination, but varied the effects of making the "correct" response. The three conditions were: (i) food reward alone, (ii) food accompanied by mild shock, (iii) food for the correct response plus mild shock for the wrong response. One aspect of his findings would have been predicted by anybody: the habit was most quickly developed under the third condition. The surprising result was the superiority of the second condition, in which shock accompanied the reward, over the first, in which only food was given [489]. There are other examples of anomalies of this sort. Brown and his colleagues trained rats to escape shock by running from a box into an alley. When trained, the rats ran from the box when they were no longer shocked there. Shock was then applied in the alley which had formerly been a refuge from the aversive stimulus. Yet the rats continued to run, although now it was into trouble instead of out of it [115]. Melvin, in experiments of similar design, found that greater resistance to extinction of a habit resulted from shock; and the more often shock was given, the more resistant were the animals to extinction [453].

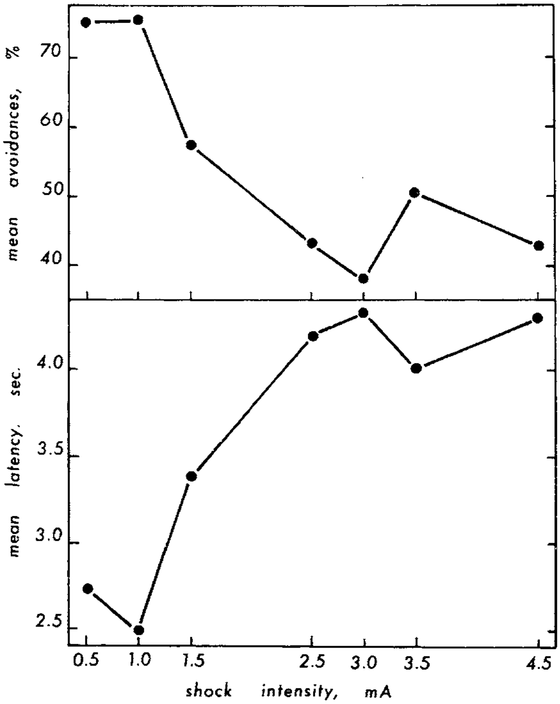


Figure 78. Increase of shock intensity above 1.0 mA leads to a decline in effective responding (upper curve) and increasing delay in responding (lower curve). (After Moyer & Korn [488].)

Punishment, then, can facilitate, instead of prevent, the performance of a punished act. How it does so is uncertain. On one hypothesis, a mild aversive stimulus in certain circumstances makes it easier for an animal to discriminate between two situations. Another, which applies to the effect on extinction, suggests that, since the animals have learned to run to avoid shock, further experience of shock simply strengthens the habit. Whatever the explanation, we need not be surprised that responses to punishment often seem maladaptive. There is probably no counterpart of the conditions of these experiments in nature: the evolutionary history of rats, as of other animals, has not equipped them to deal with enviroments in which they are liable to receive sudden electric shocks through their feet. This assumption does not, of course, help us to explain the behavior; but it provides a different frame of reference in which to think about punishment. It might even suggest new experiments, in which more natural conditions are simulated.

Indeed, as described in §§4.3.1.2 and 8.3.1.5, one more natural kind of aversive stimulus has been much studied, with notable results. If a rat has survived a dose of poison, its behavior is drastically altered: it not only tends to avoid the mixture that has caused the illness, but also alters its feeding behavior in other ways. Moreover, there can be a delay of several hours between ingestion of food and the associated ill effects; hence the assumption that *all* conditional stimuli must, to be effective, occur within a few seconds of their action on the animal, is not valid.

8.3.3.3. *"Fear" and aversion.* A rat's immediate response to shock, or even to a sudden high-pitched sound, may at first be rather ill-directed: Bolles [100] lists the immediate consequences of shock as jumping, freezing, squealing or biting. He adds: "It is difficult to know what behavior to use as an index of drive." This sentence implies, as do many other writings, the existence of a single process which regulates all the behavior evoked by an aversive stimulus. We have seen how the search for "unitary drives" has been unsuccessful in other contexts such as feeding (§4.4.3.4). Nevertheless, even if we suspect that it is certain to fail, we can learn from a similar attempt to account for the effects of aversive stimuli.

It has been suggested, notably by Mowrer [485], that two "learning processes" can be distinguished. On this view, the effects of positive reinforcement represent one kind of internal process which leads to habit formation, but the effects of punishment are due to another. If a man suffers pain in a particular place, the place itself may come to arouse fear. While habit formation impelled by an internal deficit stems from something continually with the animal until the need is satisfied, learning to avoid an aversive stimulus is inevitably related to the external conditions which accompany the stimulus. N. E. Miller gave rats electric shocks in a shuttle box, and so trained them to cross into the adjoining compartment. Each trained rat was then put in the compartment in which the shock had occurred, but with a door to the other compartment closed; no shock was now given. The door could be opened by turning a wheel or, later, by pressing a bar. These acts were readily learned by rats which had experienced moderate shocks, but not so readily by control rats which had not been shocked. The trained rats, on being dropped into the first compartment for no-shock trials, urinated, defecated and showed signs of exceptional muscular tension; these objective signs have been used as grounds for speaking of "fear" in these rats [460].

Such experiments have been held to show that "fear" is an "acquirable drive"; and that reduction of fear constitutes a reinforcement for the development of new habits. This notion can be given a physiological meaning.

Severe aversive stimulation activates the sympathetic nervous system and stimulates the secretion of adrenalin; it also tends to raise the output of hormones by the adrenal cortex (§10.2.3). If a noxious stimulus regularly follows some previously neutral occurrence, such as being put in a box or hearing a sound, the visceral change perhaps comes to be evoked by the neutral occurrence: the neutral stimulus is then a conditional stimulus and the sympathetic activity becomes a conditional response. The components of the visceral response may include increased heart rate and respiratory rate, sweating and movements of the alimentary tract. These take place also in human beings when they say they are frightened or anxious, and so we have in them objective criteria of fear and anxiety. Accordingly, when an animal learns to avoid a noxious stimulus, for instance by jumping from one compartment to another in a shuttle box, this is said to be due to an "anticipatory visceral response": the latter immediately follows the conditional stimulus, and *ending the visceral response* (by departure from the alarming situation) becomes a secondary reward for flight.

Certain stimuli undoubtedly cause immediate avoidance: cutting the skin is a simple example. Fear or anxiety, or rather the visceral responses just described, are said to act in themselves as noxious stimuli which an animal will learn to avoid if it can. Consequently, it learns both to avoid anything which has become associated with this internal state, and also to take flight whenever it finds itself in a position in which the visceral response is aroused.

There is some supporting experimental evidence. Wynne & Solomon studied the effects of shock on dogs: some had had the sympathetic nervous system removed; some had had drugs which reduce sympathetic activity; and some, the controls, had merely been subjected to shock. Both sympathectomy and drugs reduced the avoidance due to shock [727]. In another kind of experiment, Farber studied rats which had developed response fixation as a result of being shocked in a **T**-maze. A response fixation is a compulsively performed movement, such as turning or jumping always to the right, regardless of the circumstances. According to Farber, these responses come to be made and fixed because they lead to "anxiety reduction"; and this is because they take the animal away from external cues which induce anxiety on account of their association with shock. Farber also suggested that feeding would reduce anxiety; and feeding his rats in the **T**-maze, in conditions in which response fixations were ordinarily developed, did prevent the fixations [233].

On evidence of this sort, Mowrer [485] has proposed a "two-factor learning theory" which distinguishes two classes of stimuli: (i) those (response-contingent) due to an action of the animal, such as pressing a lever, which give rise to proprioceptive and other inputs; (ii) those independent of the animal, such as a noise, or attack by a predator. If a stimulus of the first category is followed by reward, the act that led to it tends to be repeated and so a habit is formed. Reward after a stimulus of the second kind induces approach to the source of the stimulus. In either case, in Mowrer's terminology, the stimulus gives rise to "hope" (anticipation of reward). By contrast, punishment of a response-contingent stimulus causes inhibition of the response, while injury associated with an independent stimulus leads to flight. In the last two instances, "fear" is aroused (that is, expectation of pain).

The anthropomorphic terms, hope, fear and even expectation, are obviously open to criticism. Hurwitz & Dillow complain that their use "stunts the growth of behavioural analysis by . . . opening the gates to old entelechies in modern dress"[342]. For more specific critical analysis, it is essential to distinguish between escaping from an aversive stimulus and avoiding it altogether. According to Mowrer, a warning stimulus comes to induce a part of the response originally induced by the aversive stimulus itself. The part induced he calls "fear"; hence, what seems to be avoidance of the aversive stimulus by the trained animal is in fact only escape: the animal escapes from an internal state.

Apart from the absence of any satisfactory physiological basis, the theory fails to account for certain experimental findings. Sidman puts rats in a bar-pressing apparatus in which they received a shock at regular intervals. The shock could be prevented by pressing the bar. If the interval between shocks was twenty seconds, it was necessary for the animals to press the bar at least once every twenty seconds to prevent shock altogether. The habit was duly acquired (figure 79), although there was no warning signal to indicate the impending onset of shock. Only being in the apparatus indicated, after the first experiences of shock, that the stimulus would continue to be received at regular intervals [608, 610].

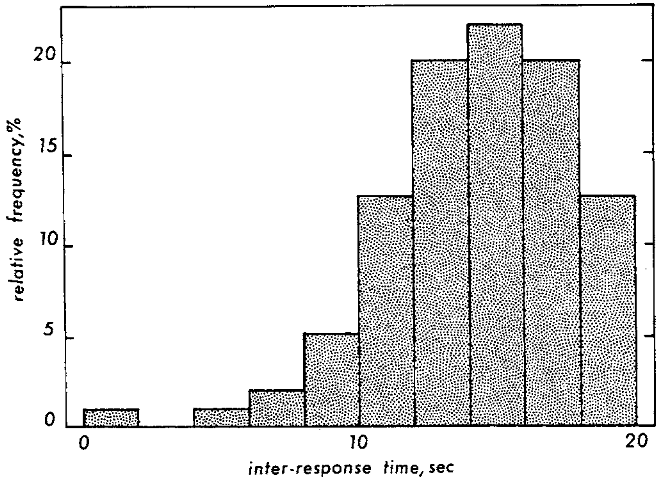


Figure 79. Sidman avoidance. A rat is trained to press a bar to prevent shock which will otherwise come on every 20 sec. The histogram gives the distribution of intervals between responses of a trained animal. (After Sidman [609].)

Sidman's primary discovery, that rats can develop an efficient habit of avoidance in such a situation, is perhaps not in itself surprising. The difficulties arise when we seek an explanation, either in terms of physiology or by invoking "fear" as a substitute for physiology. An obvious hypothesis is that the stimuli from the apparatus, present at the time of the shock, come to be aversive: this proposal, in fact, invokes a process analogous to secondary reinforcement (§8.3.1.6). Accordingly, Keehn put rats in a running wheel in which they received a shock at twenty-second intervals unless the wheel was turned. Turning the wheel postponed shock as in previous experiments. One group of rats was trained in the manner described above, without a warning signal. A second group received a warning signal just before the shock; and they were able to postpone the signal as well as the shock. If the signal had itself come to develop aversive properties, as in the hypothesis, the rats should have worked to postpone it too. But they did not do so: with training they came to respond increasingly during the warning signal rather than before it. Hence the signal had acquired no secondary aversive property [357].

Overmier has examined the question of "fear" during "Sidman avoidance training" in an objective manner: he recorded defecation rates and other features of autonomic activity: "fear" in this sense was evident during acquisition of the habit of avoidance, but not during maintenance of the habit by the trained animals. Hence, even if "fear" does play some part in habit formation, its rôle is probably less than that assigned to it by Mowrer [515]. As Hurwitz & Dillow remark, "fear" is at best only a stopgap until a better analysis is available [342].

8.4 EXPECTANCY AND SET

8.4.1. Expectancy

The hypotheses described in the preceding section include references to "expectancy"—a term which (like "fear") suggests an interpretation of behavior in terms of human feelings; but, despite the subjective implication, the concept of expectancy does refer to actual features of behavior. There are many examples of habits in which responses are made in advance of the events to which they are relevant.

The anticipatory character of some behavior was first studied rigorously in the CR (§7.2.2). Other examples follow below. Systems in which anticipation is emphasized are sometimes referred to as expectancy theories. At first sight, when shorn of jargon, they seem to state the obvious. If a man finds food in a particular place, he will probably revisit that place when hungry; he is then said to be expecting food. Information has evidently been stored in the CNS through the combined effects of the internal state and of the external situation associated with food. Finding the food confirms the expectancy, that is, puts an end to the anticipatory central nervous processes. This strengthens the habit of visiting the place when hungry.

These statements are of little use unless they can be made more specific. Animals such as rats, like men, are assumed to have what Hebb has called an "anticipatory central action" [307] during performance of a habit. As we know, the behavior of wild rats may be profoundly disturbed by an encounter with an unfamiliar object in a familiar place—that is, a place which the animal is in the habit of visiting; the disturbance is evidently a result of a contrast between the expected and the actual (§3.3). Further evidence is found in the phenomenon of motor equivalence. A rat trained in a Skinner box does not always press the lever in the same way: just as a man may turn a switch with either hand or even his elbow, a rat may use either forelimb or even its teeth; much practice is required to achieve a more constant pattern of movements—far more than is needed for uniform success in actually getting the lever depressed. Hence the process described in §7.2.1 as a gradual elimination of all but effective movements during trial-and-error is usually not complete.

Goodson and his colleagues used two food mixtures in some relevant experiments. One, of bread, milk and sugar, was preferred by their rats to a wet mash. The rats were trained in a **T**-maze. They were given experience of the preferred food in both arms of the maze; but they were then trained to go to one arm with a reward of the preferred mixture. When trained, they were offered wet mash in the arm they had been trained to visit. They turned away (one is tempted to say, "in disgust") and went to the other arm, although in other circumstances they accepted the wet mash [265].

The importance of the anticipatory process has been further illustrated by Prokasy. He used a maze with a single choice point, in which the two goal boxes were both out of sight of the rat even after it had chosen the left or right path. There was an even chance that a given goal box contained food; but on *one* side the rat could tell in advance of reaching the goal whether it would get food, since the passage was painted white when food was there, black when it was not (or vice versa). After fifteen days of training, the rats developed a preference for the arm of the maze in which they received advance information, although they got no more food on that side than on the other (figure 80). Hence, as Mowrer [486, page 188] points out, access to "information" was rewarding.

These facts may be linked with the "insight behavior" displayed during experiments on direction-finding (§7.3.4.2). This entails, to quote Hebb again, "an association with a present state of affairs and one that has followed that state of affairs (or similar ones) *in the past*" [307]. The performance of a system of movements, in a novel situation, brings an animal to a goal. Once again we observe the ability of animals to synthesize an effective action from a number of formerly separate movements. The anticipatory process in the brain is then a representation or model of the actuality which the animal has previously experienced.

8.4.2 Set

The ability to produce novel and appropriate patterns of action is one of the most difficult of phenomena to account for neurologically. It reflects a general property of the most complex nervous systems: the storage of information which makes habit formation possible also tends to improve the animal's performance in solving other problems later on. There is not only learning of new habits, but also "learning to learn"—deutero-learning [69].

Much habit formation depends on combining the effects of separate, previous experiences (§7.3.4.2). A simple kind of insight behavior is displayed when two portions of a maze have first been independently learned; but there is also a more generalized *transfer of training*. Harlow [290] and his colleagues have made a study of the deutero-learning of Primates. Koronakos & Arnold give an example from rat behavior. Rats were fasted and put in an apparatus with five doors, each marked with a pattern; four had the same pattern, the fifth a different one: in one instance four doors were marked with a rectangle and one with a cross. The door with the odd pattern was the only one unlocked; once through it, the rat was required to make another, identical discrimination to get to food. Eight oddity problems of this sort were presented; each had to be mastered to a specific criterion before the next. Out of twenty rats, five clearly improved in the ability to learn the tasks as the experiments proceeded: in them, therefore, there was transfer of training, or the formation of "learning set" [377].

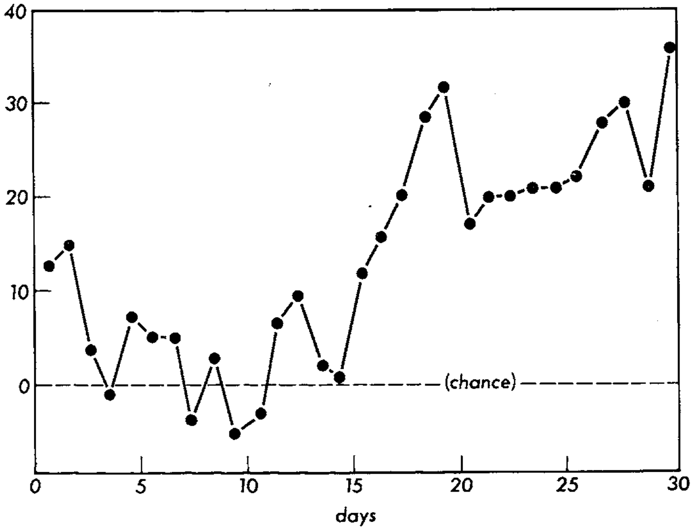


Figure 80. Expectancy. Rats come to prefer a pathway which gives them early information on whether there is reward or not, even though selecting that pathway does not lead to reward more often than the alternative. In the graph, points above the chance level show the degree of preference. See text. (After Prokasy [530].)

Manocha and his colleagues have reviewed other work on rats, and give more evidence of transfer of training [434]. Sutherland & Williams have given further evidence of a remarkable ability by laboratory rats. They trained their animals to distinguish between a regular and an irregular pattern (figure 81); later the rats were evidently able to make use of the training when discriminating between other pairs of patterns, one regular and the other with a "mistake" in it. Hence rats have the ability "to store an abstract description of a pattern" [660].

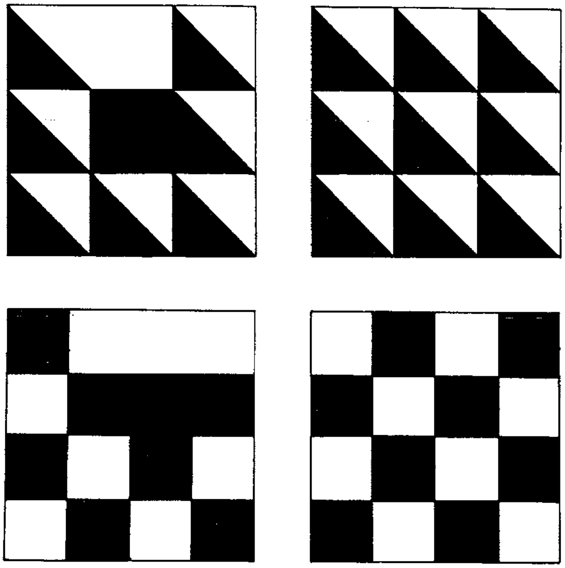


Figure 81. Discrimination and transfer of training. Rats were trained to respond to the figure at top right, but not that at top left. This type of training transferred to a general tendency to approach irregular rather than regular figures, such as those below. (After Sutherland & Williams [660].)

8.5 Extinction and Recovery

As already mentioned (§7.2.2), complex habit formation always involves inhibition as well as the development or fixing of responses. One form of inhibition occurs when a CR is repeatedly evoked without reinforcement. This phenomenon, extinction, or internal inhibition, has been much studied in trial-and-error situations (figure 82). Osgood [514, page 336] gives the example of a fasted rat in a Skinner Box. The response of bar-pressing is established by rewarding it with, say, the usual food pellet. Then the supply of pellets is cut off. The rat, after several unrewarded trials, resorts to sniffing around and biting the bar; the bar is pressed only at irregular intervals. Eventually a substantial time passes during which the rat does not press the bar once, and extinction is said to have occurred. The criterion of extinction, that is, the length of time during which the act is not performed, is arbitrary.

After, say, twenty-four hours, the rat is again put in the box, and then displays spontaneous recovery of the act (figure 83), like one of Pavlov's dogs. The internal process which produces extinction has declined, and response strength is nearly, but not quite, what it was before extinction began. Extinction is more readily achieved the more energy is involved in performing the act to be extinguished: the more effort the animal has to make during the response, the more easily it is induced to give it up (but compare §7.2.1.3).

The pattern of reward also influences the rate of extinction. The effect does not match that on the rate of habit formation. We know already that (i) the readiness with which a response is reliably developed is proportional to the incidence of reward: the higher the proportion of acts rewarded, the more quickly the habit is developed; (ii) by contrast, the extinction rate is higher when the incidence of reward is higher: a habit is only slowly lost if the animal has been accustomed to being infrequently rewarded for performing the act (figure 73). These findings show how habit formation covers a number of processes imperfectly correlated with each other.

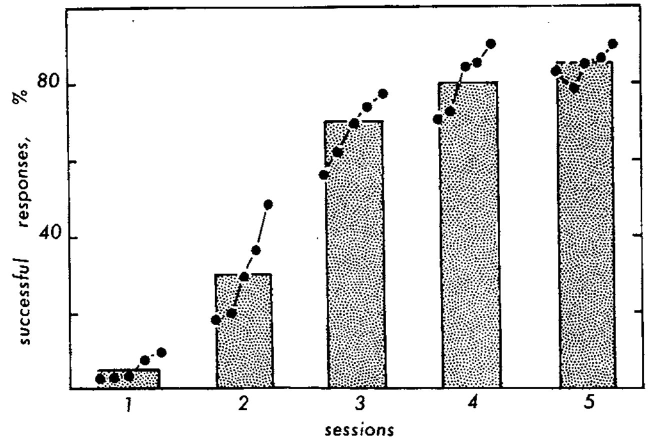


Figure 82. Extinction. Response rates in a bar-pressing apparatus after reward has been withdrawn from trained rats. At first response rate rises: extinction begins only after the third day. Vertical bars represent standard errors of the means. (After Wickens & Miles [712].)

An analogous effect is observed if the amount of reward is altered. Armus ran rats in a runway after a fast of twenty hours. Some rats had ten pellets at the end of the runway, but others were given only one. The first group, of course, acquired the habit more quickly than the second. They were then put on an "extinction schedule": that is, they were run without any food at all. Extinction of the habit was more rapid among the animals which had received the larger reward [25].

Since spontaneous recovery is never complete, an animal is evidently *learning not to respond* during extinction: as we saw in §7.2.2, extinction does not represent the undoing of a learning process in the CNS. (Forgetting is discussed below, in §8.6.) The neural basis of the two processes, learning to act and learning not to act, is unknown. Certain substances have nearly opposite effects on them: depressants such as sodium bromide, NaBr, produce slower habit formation but quicker extinction; stimulants, such as caffeine and amphetamine, promote habit formation but slow down extinction [449]; but we have yet to learn how these drugs act on the brain.

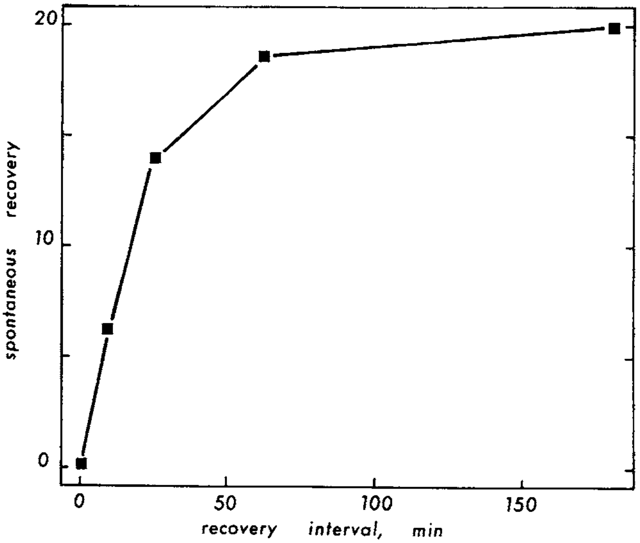


Figure 83. Recovery from extinction. When a bar-pressing habit has been extinguished by withdrawing reward, the habit recovers after a time. The curve measures degree of recovery of the habit. (After Ellson [217].)

8.6 "MEMORY"

Extinction is a corollary of the effects of reward: when reward is withdrawn, an animal acquires an inhibition against responding in a particular way. Recovery from extinction shows that the information stored during development of the original habit is hardly affected. Hence we may infer from behavior that habit formation entails at least two distinct central processes: (i) storage of information, (ii) retrieval. The first does not guarantee the second. Moreover, the storage of information is a complex process. Figure 62 illustrates how performance improves during a group of trials given on a single day—a short-term effect. But there is also improvement between days which indicates a longer-term process.

There may be yet further, preliminary events, sometimes called "registration" (reviewed by Jarvik [344]), which itself includes a number of components: they include the performance of sensory systems, and also the effects of level of arousal (§2.5).

In this section we consider especially the ways in which information is retained and lost. Colloquial terms (in this case, "remembering" and "forgetting") then become, as usual, inappropriate. We say a person remembers something when registration, retention and retrieval are all successful. The aim is to dissect memory in this sense into components which can be described quantitatively.

A first requirement is a reliable experimental procedure. Laboratory mice are often used. An animal is put on a platform near a small entrance into a dark box. Left to itself, it soon goes in: the delay, or latency, may average about ten seconds. If it is tested again the next day, the latency may be less.

But suppose it is given an aversive stimulus, such as an electric shock, on entering the box. In this case, if the animal is tested twenty-four hours later, the latency is much greater: about 70 percent of mice may fail to enter within thirty seconds. Alpern & McGaugh show that the effect on latency is evident only a few minutes after the shock, and may be retained for some weeks. They also describe a method of interfering with the effect of the aversive stimulus. They use electro-convulsive shock (ECS)—a treatment also employed clinically by psychiatrists. A singe ECS shortly after training prevents the training from having any effect: evidently, either retention or retrieval has been interfered with [14]. It might be supposed that ECS would, at least for a time, have a generally disruptive effect on behavior, but this is not observed. Moreover, the retrograde amnesia which results from ECS is usually permanent [448]. Alpern & McGaugh also describe the effects of ECS after a delay: if it is given, say, three hours after training, there is still some amnesia: the extent of the amnesia depends on the duration of the ECS. These authors therefore support the view that the full establishment of the memory trace or engram requires some hours [14]. This is the consolidation theory of memory.

Retrograde or retroactive amnesia is not forgetting: the latter is a gradual loss with time. Although the amnesia has been held to represent an interference with storage, it remains uncertain just what element in the whole complex process of habit formation is eliminated by ECS. Mendoza & Adams recorded autonomic instead of somatic responses after ECS, and found no effect of the ECS. They, and later Adams and others, have therefore suggested that ECS does not interfere with consolidation of the engram, but induces what they call disinhibition. In their view, the training has had its effect on the brain, shown by the continued autonomic responses. But the ECS somehow cancels the inhibition which the animal normally displays [1, 455].

A different, and perhaps more promising, method of studying retention is the use of drugs, reviewed by McGaugh & Petrinovich [449]. ECS always impairs performance; some drugs improve it. For example, mice may be trained in a visual discrimination: under food reward, they come to choose the correct of two alleys (painted white or black) nine out of ten times. During training to this criterion, controls make about twenty errors. In one set of experiments, three training trials were given on each day, and the experimental groups received a drug after the third trial on each day. Some drugs, such as strychnine, reduced the number of errors to about five. The drugs have maximum effect if administered during the fifteen minutes immediately after training. Strychnine also counters the effects of ECS: if the drug is given about ten minutes before the animal undergoes training, ECS given one minute after training has no effect. Amphetamine has a rather similar action: rats trained to avoid shock retain the effects of the training better if they are given amphetamine just after a training session [226]. Garg & Holland have studied consolidation in the formation of a maze habit. They used two strains of rats, reactive and non-reactive, and the Hebb-Williams maze (§7.3.4.1). Giving the rats picrotoxin after each trial reduced the number of errors made during training, especially by the reactive rats. By contrast, pentobarbital sodium, similarly administered, increased errors [253].

These are examples of how the short-term components of memory may be analyzed. Other, longer-term processes are discussed elsewhere: they include habit-formation with a long delay between associated events (§8.3.1.5) and the effects of experience in early life on adult abilities (§8.7.2.2).

8.7 ONTOGENY

8.7.1 Effects of Age

The belief that one cannot teach an old dog new tricks is a firmly established old wives' tale. Unfortunately, it is not as readily tested as might be supposed, even if rats are substituted for dogs. Most of the measurable features of an animal change with time, and the changes are only imperfectly correlated. It is not possible to hold all these properties steady except the one to be studied. C. D. Williams and his colleagues recorded movement in a **Y**-maze, and found a peak of activity at eleven weeks [715]. Candland & Campbell have similarly described effects of age on avoidance of shock ("fear") and exploratory movements in an open field [134]. Such changes could influence what Campbell [128] calls "the basic ability to learn and to retain learning"—a phrase that itself illustrates some of the difficulties: to make it operational, it must be equated with some actual performance, such as developing the bar-pressing habit, or learning a maze, each in specified conditions. Different measures of habit strength may then prove to be differently correlated with age: Campbell & Campbell found no difference between eighteen-day and hundred-day rats in extinction of an acquired avoidance; but the older rats retained the habit for a longer interval without practice [129]. The last finding is the opposite of what is conventionally expected.

When two classes of animals are compared in the ability to form habits, the relevant internal states of all individuals are, as far as possible, made the same. If the subjects are to be rewarded with food, the duration of fast is uniform; or the animals may all be made to undergo the same percentage loss of body weight. They are then perhaps said to be equally motivated. Campbell [128], in a search for equivalent motivating conditions, was obliged to use "intermediate ranges of electric shock" as a means of inducing habit formation. He and his colleagues used a modified type of shuttle box. Rats were trained at the ages of eighteen, twenty-three, thirty-eight, fifty-four or a hundred days. The training consisted of putting the animal on one side of the box (painted black or white), and giving it a series of unavoidable shocks. It was then put for a similar period in the other half of the box, which was painted in the alternative color; here it received no shock. Testing was carried out 0, 7, 21 or 42 days after training. The animal was now placed in the box with the partition between the two halves removed. The measure of retention was the time spent in the safe part of the compartment. The two oldest groups showed no effect even of a delay of forty-two days; by contrast, the two youngest groups rapidly lost (forgot) the effect of training.

The method used in these experiments is unusual: the animal has no opportunity to escape, still less to avoid, shock during training; it does, however, store information which can influence its behavior on a later occasion (compare §3.4.1). The findings confirm those of Stone who, on the basis of a substantial series of experiments, concluded that from the age of seventy days the ability to develop habits remains constant for many months; at earlier ages, previously acquired habits were more easily discarded [654–55].

Further work by Campbell [128] showed that young rats could retain the effects of training well if, by additional experience of shock, they were occasionally reminded of their early training. Clearly there is much more to be found out about the effects of age on the storage of information and on the development of motor habits. The work cited above suggests two general conclusions. First, nothing, however apparently obvious, can be assumed about changes with age. Second, the need for exceedingly rigorous experimental design puts a heavy demand on the experimenter.

8.7.2 Effects of Early Experience

8.7.2.1 *Imprinting.* In ordinary language, the preceding section is on the development of intelligence: the sort of question asked is: At what age can a rat most readily "learn new tricks"? We now turn to effects of early experience on later habits.

There may be only one, sometimes brief, stage or *sensitive period* in the life history, when normal social attachments can be reliably developed (reviewed by P. P. G. Bateson [70] and Sluckin [615]). Among both mammals and birds, the extent of dependence on early experience varies with the species. A general rule is: if we observe a species-typical pattern, say, of mating or of parental behavior, we are not justified in assuming that it develops regardless of the early social experience of the animal. The best studied examples are of *imprinting.* This is the process by which a young animal comes to behave in a filial way toward an object: recently-hatched nidifugous birds readily learn to follow almost anything that moves, but they later lose this propensity. A similar *following response* is undoubtedly displayed by mammals, but it has been less studied. Rats are altricial, that is, immobile and nest-bound in their early days, and therefore do not follow their mother during the early suckling stage of close attachment to her. Guinea pigs, *Cavia,* with their longer gestation, are more mature at birth, that is, precocial. In them, Sluckin & Fullerton have found evidence of typical imprinting: at the age of about a week, they can be induced to follow a tennis ball or a striped cube. The effect of this early training on adult behavior, if any, remains to be discovered [616–7].

The social behavior of laboratory mice can be influenced by early treatment. Mainardi and his colleagues used a cage divided into three compartments, connected by holes. A female was placed in the center, and a male in each of the other compartments; the males were prevented from going through the holes by means of collars or ruffs around their necks (figure 57). The female had freedom of movement and a choice of males, and the time she spent with each partner was recorded automatically. A series of experiments revealed an effect of early experience on female sexual response. Females of the sub-species *Mus musculus domesticus* avoid male *M.m. bactrianus* only if they grow up in the presence of both sexes of their own subspecies: evidently, discrimination is influenced by some property, presumably odorous, of their father (or uncles). The effect of odors was tested by perfuming the parents of young mice with Parma violet (an extract of *Viola odorata*); controls were reared by unperfumed parents. As adults, the mice were given a choice between perfumed and untreated sexual partners. The males were indifferent; but the females reared with perfumed parents preferred perfumed males, while the control females preferred normal males [429–30].

Marr & Gardner similarly exposed rats aged two to thirty days to an eau de Cologne with a strong scent: both the young and their mothers were rubbed daily with this cosmetic; controls were rubbed with odorous matter from their own cage. The young were tested in a **Y**-maze (figure 18) at thirty to forty-five days: those exposed to eau de Cologne preferred its odor to that of normal rats; the controls preferred conspecific odor [437]. Perhaps experimenters in this field should eschew after-shave lotions.

These observations remind us again of the importance of odors in the social lives of rodents (§§6.1.2, 8.2.4). They are also consequences of a kind of long-term storage of information (or memory) about which little is yet known.

8.7.2.2. *Deutero-learning in early life.* Another effect of information stored early in life is less specific. As we saw in §8.4.2, solving one problem can improve the readiness with which other, similar problems are solved. The scope of transfer of training is found to be even greater when effects of early experience are included. The method has been to rear young rats in diverse environments and to observe their ability to acquire new habits as adults (reviewed by Horn and others [333], and by B. Meyers [456]). Hebb [307] proposed an important hypothesis when he suggested that much of the storage of information ("learning") that goes on in very early life differs from that which, later on, enables an animal to adapt itself quickly to new circumstances: he describes the early process as both inefficient and slow, and yet responsible for the efficiency of later habit formation; at this stage no insight behavior is, or can be, displayed.

In an early study by Hebb, rats reared in the dark took longer than controls to learn a simple visual discrimination. But the effect soon wore off: after only one hour the rats' behavior was normal [304]. Long afterwards, Tees carried out a parallel experiment on auditory restriction. He reared rats with plugs in their ears for the first sixty days after birth. There was no effect on discriminating frequencies, and so in this respect the effect did not parallel Hebb's findings; but the experimental animals did display an inferior capacity to discriminate auditory patterns [662].

Most of the detailed work, on just what sort of early stimuli are important for later performance, has been on vision. Gibson & Walk exposed rats from birth to black triangles and circles on white cage walls; the cages of the controls were unadorned. The rats were later required to discriminate circles from triangles: the experimental group did so more quickly and with fewer errors than the controls [258]. This was evidently a purely sensory effect. Forgus studied the relative importance of sensory and motor experience (figure 84). One group of hooded rats was given much early visual and motor experience in a large and complex environment; a second group had similar visual experience but much less opportunity to move about. When the rats were tested, as adults, in a maze, the second group did better if the lights were kept on; but the first group did better in darkness, that is, in conditions in which their movements had evidently to be based on kinesthesia.

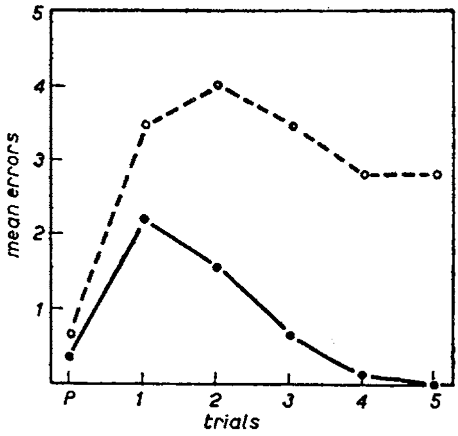


Figure 84. Effect of early experience. Rats of group 1 (lower graph) had had much visual and motor experience in early life; those of group 2 (upper graph), only visual experience. The graphs show the mean errors during successive trials in a complex maze in the dark. P stands for preliminary trials. (After Forgus [239].)

A further question studied by Forgus concerns the precise age at which diversity is experienced. He gave rats the opportunity to see a number of shapes and patterns from sixteen days (when their eyes opened) to forty-one days; another group were similarly exposed from forty-one to sixty-six days. Both were later tested in conditions demanding discrimination or generalization of shapes, and both did better than controls which had received no early "training"; but the first group, with the early experience, did better than the second [238–40]. The optimum age for the beneficial action of experience has to be determined for each type of situation. Nyman, too, gave young hooded rats experience of a complex environment: they received this treatment at thirty to forty days, fifty to sixty days, or seventy to eighty days; controls were kept in the usual small cages. The test consisted of a complex spatial discrimination. All experimental groups were superior to the controls;

but the highest score was that of the group stimulated at the intermediate age of fifty to sixty. Further diversity of experience when the rats were adults had little or no effect [503].

8.8 REVIEW

Individual adaptability to changing conditions is displayed by all animals; change of behavior in response to stimulation can be observed in most. Such modified behavior is at its most complex among mammals. Of this group, rats have not been shown to be especially notable for their "intelligence"; but they display all the conventional categories of habit formation. The factors that influence habit formation have been revealed mainly in trial-and-error situations in the laboratory. Sensory information of any kind, from external or internal sources, can be used; and inhibition, extinction and reinforcement, first systematically demonstrated by Pavlov in CRs, are displayed also in trial-and-error behavior. The rôle of the internal state ("motivation") is evident in both kinds of situation.

Trial-and-error, however, gives much more information about the learning process than the Pavlovian method: it allows the animal to display a variety of movements ("appetitive" behavior) and so to acquire new patterns of activity. A new pattern is a rule established only when performing it is accompanied or followed by reward, or by avoiding or escaping from stimulation; alternative patterns not so rewarded are given up.

This process involves *selection* of the stimuli to respond to; other quite different stimuli come to have no effect (habituation). Selection of some from among a number of similar stimuli is the important process of discrimination. But the opposite process also occurs: a response may generalize to stimuli which resemble the original one but depart from it quite substantially. The process of selection falls entirely outside the traditional concepts of learning by association; and the notion that habit formation ("learning") in general can be described in terms of Pavlovian conditional reflexes is quite erroneous. In particular, insight behavior involves the use of two or more previous experiences in the performance of a novel sequence of acts. There then seems to be an "anticipatory central action" or "expectancy" concerning the consequences of further action.

One kind of incentive to acquire new habits is avoiding pain externally caused. Avoidance is often achieved by flight, but can lead to acquisition of a more specific response. Aversive stimuli may result in generalization of the fear-and-flight response to the whole situation in which the stimuli are met. If flight is prevented, severe disturbance of behavior may follow the stimulation (§10.4). By contrast, mild aversive stimuli can sometimes, paradoxically, strengthen a habit instead of weakening it.

Since habit formation in the laboratory depends on reward, and since some of the most effective rewards satisfy bodily (homeostatic) needs, it has been proposed that learning takes place only if there is reinforcement. But storage of information in the CNS can take place during exploratory movements, without reinforcement: this becomes evident when exploratory learning is observed. Further, the variety of incentives which promote habit formation do not all directly contribute to survival, either of the individual or of the species. Although natural selection may be assumed to ensure that behavior tends to promote survival within a certain range of conditions, it does not follow that it will do so in all conditions.

The importance of storage of information, such as that which occurs during exploration, has been further shown in studies of the effects of early experience: in infancy a mammal gradually stores information that enables it to develop new, adaptive habits rapidly and effiiciently in later life; this deutero-learning is aided by subjecting a young mammal to a spacious and diverse environment.

The problems of "learning" are among the most difficult and the most important in biology. Research in this field has not yet taken any single major direction. At present its strength is in heterogeneity. Indeed, diversity is increasing. The period of ringing the changes on "schedules of reinforcement" is over. On the one hand, those primarily interested in overt behavior are widening their scope by studying new species. On the other, physiological analysis is rapidly developing greater power and refinement.

9 "Instinct" and "Drive"

Nature's great law, and law of all men's minds?
To its own impulse every creature stirs.

Matthew Arnold

9.1 THE CONCEPT OF "INSTINCT"

The word "instinct" is an echo from the past still heard in colloquial speech. It usually refers to rather mysterious human or animal abilities: its meaning, always vague, has been allied to that of intuition, and still is so allied in ordinary language. One of Darwin's contributions to the study of behavior was to encourage the rational study of the most complex and inexplicable activities of animals. Among them are the exquisitely patterned actions which enable some species to fit their lives with extraordinary precision to specific habitats or modes of existence. Rats do not provide good examples: they do not make elaborate constructions like those of beavers or bees; nor is their behavior adjusted to any special source of food, or to any narrowly restricted range of environments. Not all rodents are so adaptable. Different species of deer mice, *Peromyscus*, have been shown experimentally to respond differently to artificial environments with the visual properties of woodland or grassland respectively. V. T. Harris displayed this difference by offering mice of two species a choice between an artificial "wood" and an artificial "field": each species chose the laboratory environment that resembled its natural habitat. Thus he demonstrated a species-typical responses to visible patterns [296]. Other studies of habitat selection by closely related, partly sympatric species have been concerned in the main with interactions between the species, especially competitive exclusion. To interpret these relationships fully, it is necessary to take into account the ontogeny of preferences for different habitats. P. R. Grant studied one species each of *Microtus* and *Peromyscus* and two of *Clethrionomys* in the laboratory. Not all the members of a given species had been reared in the same habitat. Grant's important finding, for our present purpose, was of an effect of early rearing on choice of habitat. Exposure in early life to particular environmental features may, from this work, be crucial in determining adult preference [269]. Hence, once again, responses which, in an earlier period, would have been assigned to the unanalyzed category of "instinctive" or "innate" behavior, are now seen as having both genetical and environmental components in the variation they display (compare § 11.4).

Species of rats, too, undoubtedly differ in their habitat preferences. *Rattus norvegicus* is a burrower, and tends to move down rather than up when taking cover. *R. rattus* commonly lives in trees or roofs, and tends to flee upward. But the success of both species seems to depend more on their adaptability to a remarkable variety of diets and circumstances. This, with their combination of exploratory behavior and avoidance of novelty, which has enabled them to achieve so much in human communities, is the best example of special behavioral "adaptation" that they display. *R. rattus* can even occupy sewers in the absence of its congener [114, 187].

Where serious ethological writings use the word "instinct" today, it may refer (i) to some stereotyped activity, (ii) to some more general behavioral propensity, or (iii) to something inside an animal which impels it to behave in a certain way. Because the word has been used with such a variety of meanings, with much resulting confusion, it is not used in this book. This is a matter of *convenience*. It would be logically proper to stipulate a definition for the word, and to use this meaning throughout; but psychologically this procedure would be questionable. The term "instinct" has different associations for different people; in some students of behavior it arouses resistances which might preclude attention to the actual meaning of any passage in which it occurs. This is an additional reason for avoiding the term. But this does not at all entail neglect of the facts or concepts which are commonly discussed under the heading of "instinct"; and it is to these that we now turn.

9.2 SPECIES-TYPICAL PATTERNS AND PROPENSITIES

9.2.1 Patterns of Movement

It is sometimes possible to predict accurately how a rat will behave, without knowing anything detailed of its previous history: one may need to know its sex, whether it is mature and, if a female, her reproductive state, but not whether the rat has previously encountered the situation in which it is being observed. The prediction may be only of the direction of movement in relation to an object, for example, toward a burrow or another rat. But detailed prediction may sometimes be made of a sequence of movements, or fixed action pattern. Most animal species display standardized forms of movement which are characteristic in the same way as structures. These stereotyped patterns are said to be species-typical, but they may be shared by related species. Examples are given in Chapter 5: all the components of social interactions there described are shared by *Rattus norvegicus* and *R. rattus*, and some have been recorded in *R. villosissimus* [54, 146]. The same probably applies to the patterns of maternal behavior.

The most easily observed stereotyped movements, those of respiration, locomotion and eating, are so obvious that they are often overlooked. They illustrate the relationship between reflexes and more complex behavior. Respiratory movements are often described as "reflex"; eating involves the reflex secretion of digestive fluids and movements of the alimentary tract; locomotion depends on a system of proprioceptive reflexes from all the moving parts. (Indeed, all motor activity—as we saw in § 2.1—depends on a feedback of information from the effector organs.) Reflexes are little influenced by fluctuations in internal states; they are simple, although they may involve many muscles contracting and relaxing in a delicately co-ordinated way; they are standardized; and they show little improvement with repetition. They differ from fixed action patterns in their relative independence of internal state and in their simplicity. Reflexes are always components of complex sequences, as they are of all behavior; and the same reflex may appear in many patterns. But complex stereotyped behavior has a quality not possessed by typical simple reflexes: the readiness with which complex activities are performed varies with the internal state of the animal; sometimes it depends on the lapse of time since the act was last performed. This is obviously true of eating. Simple reflexes are usually set off by an immediate, standard, sensory input (as when food in the mouth evokes salivation). By contrast, complex stereotyped behavior becomes decreasingly selective in the stimuli which evoke it, as time elapses since it was last performed [324].

The movements of respiration illustrate the fact that, nevertheless, the boundary between complex patterns and reflexes is blurred. Usually, respiration is left to the physiologists, though the respiratory rate may be used as an index of "emotional state" during studies of behavior. But, as Spurway & Haldane show, even respiration can, in special cases, be analyzed in ethological terms. An air-gulping animal, such as a newt (*Triturus*) or the climbing perch (*Anabas*), has a phase which resembles searching, when it is rising to the surface. The stereotyped act is taking in air, analogous to the act of eating or drinking. The control of breathing depends on negative feedback: the greater the rate at which oxygen is used and carbon dioxide evolved, the greater the incidence of rising and gulping [639].

9.2.2 Homeostasis and Behavior

Activities such as respiration and ingestion are short-term necessities for individual survival. Such behavior is sometimes said to be homeostatic in function. Each inspiration is evoked by the slight accumulation of carbonic acid in the blood, which acts on the brain stem: the subsequent expiration removes carbon dioxide and so helps to maintain the carbonic acid content of the blood within narrow limits. This is a standard example of homeostasis, or the maintenance of a steady internal state. The corresponding facts concerning ingestion have been discussed in § 4.4.

Another example is thermoregulation. Rats are homeothermous: that is, they keep their deep body temperature remarkably steady (at around 37°C). Behavior contributes to temperature regulation. As we saw in § 6.2.2, nest-building may be important in preventing heat loss, although the nest-building of pregnant and parturient females is largely independent of external conditions. Hence nest-building has a homeostatic function but, when performed by a female, it represents an "autonomous" process. This example illustrates how a species-typical sequence can be diverse in both function and causation. The same applies to huddling (§ 5.2.1). Rats can also acquire a novel habit with warmth as a reward. Figure 55 shows a form of Skinner box in which depressing a panel switches on a heat source. Rats learn to depress the panel at a rate corresponding to need.

Behavior is also important in adapting to high temperatures. Rats do not pant, like dogs, and on most areas of their skin they have no sweat glands; but, as Hainsworth and others have shown, rats salivate copiously if exposed to an ambient temperature around 40°C, and spread the saliva by licking their bodies [278]; males pay especial attention to the bare skin of the scrotum; the hands and feet are also much licked. Rats also lie in a splayed out position that evidently allows maximal heat loss from the surface and requires minimal heat production. Again, they can learn novel habits to achieve cooling. Epstein & Milestone arranged that, if their rats pressed a bar, a fine shower of water was released. At an ambient temperature of 40°C the rats took many showers. Some of the rats at this temperature had denervated salivary glands, and so could not cool themselves by spreading saliva. Without showers, the colon temperature went up to a lethal figure; with showers, the rats learned to keep a steady body temperature [221].

Since standard sequences are often performed in response to highly specific stimulation, there must be correspondingly stable sensory arrangements: the stimulus must have a representation in the central nervous system. In chapters 5 and 6 examples are given of social signals which seem to have fixed effects regardless of experience. But there are also stable sensory organizations which have no corresponding special motor pattern. This may be inferred from behavior: the behavior, instead of consisting of a predictable pattern of movements, such as coitus or attack, may be the adoption of a particular direction of movement or even the cessation of activity. For instance, a rat may become quiescent on attaining a particular skin temperature.

A possible (but not proved) example is the effect of the odor of a predator: Griffith [272], and later Curti [182], have suggested that rats "freeze" on their first encounter with a cat. Stevens & Saplikoski have tested the hypothesis that wounded tissues produce a fright-substance, that is, a pheromone that induces withdrawal or avoidance. This seems unlikely at first sight, because rats readily eat other, dead rats. The apparatus was a straight runway, in which laboratory rats were trained to run for water. Muscle or blood from suffocated animals, placed on the runway floor, evoked a number of responses, including freezing, urination or defecation, turning away and agitated behavior when later handled. Brain tissue had some of these effects. The authors suggest that the active substance is produced only when the donor has been "stressed" [649].

Yet a further kind of sensory ability, required for adapting movement to distance, has been described in § 6.3.1. "Cliff-drop aversion" is evident very early in life, and certainly does not require prolonged training. The neural organization involved must be complex. Walk [698] has reviewed the evidence on just what feature of the situation induces avoidance. There are at least two possibilities. Consider the situation in which the floor at the bottom of the "cliff" (figure 58) is patterned. The further away the pattern is, (i) the more elements of the pattern are seen at once, (ii) the more slowly the elements move across the field of vision when the animal moves its head. Evidently the second ability, that is, response to motion parallax, develops without practice: even rats reared in darkness can make use of motion parallax as soon as they are put, in the light, on an experimental platform [259].

9.2.3 The Importance of Ontogeny

The examples described in the preceding sections show that rats, like other animals, possess a repertoire of typical behavior patterns and sensory arrangements which (i) have obvious survival value and (ii) seem to be remarkably stable in development. In their stability they resemble structural features such as the form of the ear or tail (both used in classification), or chemical effects such as hair color. Variation in all these features *can* be environmentally determined. The important general principle is contained in the phrase "stable in development" [326]. It is not appropriate to say that these behavior patterns are "genetically coded"; nor should they be thought of as "inherited" as if they were items of property. All behavior is influenced by both the genome and the environment. The term "phylogenetically pre-programmed" has also been used, to emphasize that the behavior is a product of natural selection and was perhaps performed in the same fashion in the remote evolutionary past; but the comment must be made once again that all behavior, whether fixed or adaptable, is subject to natural selection. The important distinctive feature of a species-typical action pattern, or of so-called innate behavior, lies in its ontogeny. The fundamental biological principle is that of epigenesis: that every feature develops anew in each individual. It causes great difficulty, and is further discussed in chapter 11.

9.3 THE CONCEPT OF "DRIVE"

The concept of instinct embraces much more than the performance of stereotyped behavior, however complex. Behavior is often most easily described in terms of the end attained. A fixed action pattern commonly comes at the end of a longer sequence. A rat feeds after it has moved from its sleeping place to food; movement is direct if the food is where it has been found before; if not, movement is wide-ranging. Similarly, if a rat is disturbed, it may or may not be able to run straight to cover. When the end point is food, the act of feeding is an example of a fixed action pattern, but the preliminary movement is of a different character. The difference is not in the locomotor movements themselves (since they are stereotyped), but in their relation to the surroundings of the animal. The movements preliminary to eating, mating and other essential activities fall into no standard pattern; they are therefore often difficult to predict, even though the end is not.

We have then the situation (already discussed from a different point of view in chapter 3) in which behavior is variable but nevertheless seems directed by a goal that is easily identified. The sequence is as follows: (i) an internal change takes place, for instance, a deficit develops, such as that due to deprivation of food; (ii) preliminary, unstandardized ("appetitive") movements are performed; (iii) a stereotyped activity, sometimes called a consummatory act, is carried out; (iv) the deficit is abolished and a "consummatory state" is achieved.

Accordingly, every act performed by an animal, and every failure to respond to a stimulus, raises the question of what makes an animal either responsive or immobile. The vague term "motivation" may be used in reference to internal processes which influence activity. The need for a concept of motivation arises from the fluctuations in an animal's responsiveness, which can occur independently of changes in its surroundings. A female rat on one occasion allows a male to mount her; on another, she ignores him or kicks him off. A fragment of food is eaten on one occasion, but a similar fragment, on another, is used for nest-building. These changes are not examples of habit formation: they are independent of special previous experience. They are sometimes, as we know, described as representing alterations of "drive"; and we must now analyze this notion.

The relevant *facts* may be put in three classes. (i) First is the spontaneity of behavior: a sleeping animal wakes, grooms itself and moves off to a source of food or water, although there has been no change in its surroundings. Similarly, we have the alterations in attitude to food or a mate mentioned above. (ii) The consequent "directiveness" or "goal-seeking" tendency is most clearly expressed in the persistence of activity until a particular state is attained, or when—as a result of a previously formed habit—a particular path is chosen from a number of alternatives. Another kind of persistence may be displayed on removal of a stimulus: the animal moves around until it once again finds the lost object. (iii) Some fixed action patterns form groups, of which all the members are activated at the same time: an obvious example is the group of activities displayed by a female with young; another is the simultaneous development of sexual potency and threatening behavior by a male. Simultaneous activation suggests that the different patterns have a common source.

As Hinde has shown, the contexts in which the term "drive" occurs imply at least two meanings: (i) it may refer to the state of internal organs, usually no doubt the CNS; but (ii) it may also refer to internal agencies (less often, external ones) which influence the state of the CNS. The first meaning is usually implied in the common use of expressions such as "hunger drive" and "sex drive": here the internal processes referred to are those especially responsible for particular kinds of behavior. A similar meaning is found also in phrases such as "general drive state": while the behavioral index of "hunger drive" is usually the readiness with which an animal will eat, "general drive" concerns total activity. The status of the term "drive" is in fact similar to that of "instinct" [325].

Even if the term "drive" is ambiguous, there is still the question: Can the various phenomena to which it is usually applied be given any unitary explanation? More than a century ago Herbert Spencer wrote of "nervous energy" and "nerve force"—phrases taken up by Darwin in *On the Expression of the Emotions*. Both assumed as an "unquestionable truth" that there was something that could properly be called "nerve force" which built up and was obliged to "expend itself in some direction" [184]. Today physiologists deal (as a rule) with substances and forms of energy which can be unequivocally identified and accurately measured; but unfortunately some writings in the behavioral sciences still cling to unidentifiable entities. This is the source of a number of mechanical analogues applied to the build-up of "drive" (that is, readiness to act) that sometimes occurs when an animal has no opportunity to perform an activity such as eating or coitus (reviewed by Hinde [325]). In one form of hydraulic model, a reservoir fills gradually until a threshold is reached, when the machine or animal will perform some act, provided that an external releasing stimulus is present; to parallel, even faintly, the facts of behavior, would require a *tour de force* of plumbing.

There has been much discussion on the significance of these models, but critical scrutiny soon shows them to be no more than metaphors with the only function (if they have a useful function) of enlivening descriptions. Nevertheless, there are many examples, both in behavior and in physiology, of regular increases in responsiveness, and also of threshold values. There is, for instance, the build-up of central excitatory state in a neuron until the cell discharges and an impulse is produced in its axon. The reservoir model, indeed, does include one feature which is accurately paralleled by certain events in the body: Haldane has pointed out that the readiness of a center in the brain to produce nerve impulses may depend on the accumulation of substances; carbon dioxide in the blood has just this effect on the respiratory center [281]. In the hypothalamus there are the centers which regulate ingestion and other bodily processes; these may be sites at which accumulated substances are active (§ 2.6).

Hypotheses about the accumulation of substances sometimes try to account for both the initiation of an activity and its ending; yet in fact activity often ceases, not as a result of exhaustion of a substance or source of energy, but because a particular input reaches the CNS. Swallowing food can have a satiating effect even if the food fails to reach the stomach; and the mere inflation of a balloon in the stomach may similarly reduce readiness to eat (§ 4.4.3.2). Similarly, during coitus, orgasm ends activity as a result of inhibitory afferent impulses. These are examples of peripheral switching off effects. Accordingly, the impulse to act or to become immobile should not be treated as if it were due to any single process.

This is especially clear from the facts already given on feeding. When brain injury induces hyperphagia, the excessive eating is fully expressed only when food is easily accessible. If the animals have to work for food, they show, in the words of Teitelbaum [665], "a *lower*-than-normal drive to obtain food" [emphasis added]. To talk about feeding behavior ("hunger drive"), for example, as if a single mechanism were responsible for seeking food, beginning to eat it, continuing to do so and finally stopping, is inappropriate.

There are other aspects of the plurality of drive-phenomena. Activity is not reduced *only* when some direct advantage is achieved. This is the case with exploration: a rat's tendency to explore declines as exploration proceeds, even when nothing useful has been found (§ 3.2.3). There are also the many instances of incomplete performance of a consummatory act being followed by a decline in activity ("drive reduction"). In work already cited (figure 76), sexually inexperienced male laboratory rats were allowed to copulate with females, but were removed before ejaculation occurred. This proved to act as a reward for the formation of a habit, even though it was also followed by disturbed behavior.

To sum up, the phenomena discussed in this section, when examined in detail, do not support a simple interpretation. Nor is it appropriate to ask: What is "drive"? Once again, we have to look for the facts. And then, instead of trying to bend the facts to fit existing language, we have to attempt a description, in plain words, of what we find when we look.

10 "Emotion" and Pathology

. . . We may conclude that the philosophy of our subject has well deserved the attention which it has already received from several excellent observers, and that it deserves still further attention, especially from any able physiologist.

Charles Darwin
(On the Expression of the Emotions in Man and Animals)

10.1 INTRODUCTION

There is a rather heterogeneous group of activities all of which may be called "abnormal": this term has many meanings, including "atypical"; "departing from the mean"; "unnatural"; "diseased"; "biologically disadvantageous"; and others. Here we are concerned with activities and processes which often *seem* (from the point of view of survival) to be inappropriate to the needs of the animal or species; but a decision on whether they are useful, neutral or harmful is often impracticable, since we do not know all their causes or their effects. If we see a dog panting with its mouth open, we may infer that it has just taken vigorous exercise; but the dog might merely be cooling itself; or it might have been subjected to conditions, other than exercise or heat, that arouse autonomic and allied activity ("anxiety" as described in § 8.3.3.3). If the panting is due to the last cause, we may regard it as a by-product of mobilizing the body for action; but we cannot be certain that this is its only significance.

Whenever a resting animal is roused to action, the rates of many bodily processes are increased. The increase occurs even when the action is related to the maintenance of internal constancy of certain features (homeostasis), for this may demand substantial changes in other features. The changes include those that, in man, accompany fear or anxiety, as reported by volunteers in laboratories or patients in consulting rooms [323]. Some reflect increased activity of the sympathetic nervous system. These include sweating (by those mammals, which, unlike rats, have a full complement of sweat glands), and tachycardia; there are also increases in blood pressure, in blood glucose and in pulse and respiratory rates; and there is usually pilo-erection and dilated pupils (mydriasis). Some of the signs, however, are of parasympathetic origin: they include evacuation of the bladder and rectum which, as we saw in § 5.3.4, are displayed by a resident wild rat about to attack an intruder.

Some of the signs, which we usually associate with severe disturbance, can be observed when an animal is only mildly active. Steinberg & Watson, as already mentioned (§ 5.4), have studied the effects on rats of merely moving them to an unfamiliar environment: at first, they eat less and lose about 10 percent of their body weight; but daily administration of chlorpromazine hydrochloride (a drug used clinically as a tranquilizer) prevents most of this loss [646]. As Olds has remarked, there is a spectrum of responsiveness from attention, through fear or anxiety, to panic, which parallels changes in the nervous system [509]. Here, of course, we are concerned, not with emotions which we observe in ourselves, but with the measurable features listed above—features which can be recorded, as far as we know, in any mammalian species.

The pioneer in this objective study was W. B. Cannon, whose account of the activity of the sympathetic nervous system and of the adrenal medulla, with their effects in the body, has long been familiar. He emphasized that the bodily changes in "pain, hunger, fear and rage" are adaptive: they increase the animal's capacity for violent action, needed in flight from an enemy or in attacking prey. This obviously holds for the increased blood supply to the skeletal muscles, the higher breathing rate and the raised blood glucose. Further study has added complexity to Cannon's scheme [255]. The sympathetic and parasympathetic systems may be distinguished anatomically and by the different sets of drugs which imitate their actions, but they do not always act in opposition. The fact that, in an emergency, an animal may defecate and urinate in an atypical fashion shows that parasympathetic excitation may occur in situations where sympathetic activity is also increased. Some consequences of parasympathetic action are clearly appropriate for vigorous activity: vagal stimulation results in release of glycogen from the liver, and so increases the ability of the animal to maintain a high level of blood glucose. This occurs even when rats are attacked by conspecifics: such rats tend to be hyperglycemic, but their liver glycogen is low [51].

The quotation from Olds above suggests that arousal at an extreme level ("panic") is maladaptive. It also implies the existence of an optimum level for the processes covered by such vague terms as "arousal" and "emotion" or "drive state" (reviewed by Leuba [411]). There is evidence of the existence of optimum deficits for habit formation (§ 8.3.2), but much uncertainty remains. One difficulty becomes evident if we attempt an analysis of the concepts of emotion.

10.2 "EMOTION"

10.2.1 The Open Field

We saw in § 3.3 that, while rats are compulsively exploratory, wild rats also display a marked neophobia, or avoidance of new objects in familiar conditions (sometimes loosely referred to as "fear"). Sometimes laboratory rats, too, act in a way which would colloquially be called fearful. Even in scientific writings, the behavior may be said to measure "emotionality": the experimental procedure is usually to pick a rat out of its cage, and to place it on a flat, circular or square featureless surface, that is, an open field. The arena may resemble a table top, or it may have walls. It is usually marked out in smaller areas, so that the animal's gross movements can be recorded by an observer. Commonly, the animal is left there for only a few minutes. During this period, (i) the time spent motionless ("freezing"), (ii) the distance traveled, and (iii) the number of fecal pellets deposited, are recorded.

The procedure is easy and inexpensive. Unfortunately, the findings it yields are difficult to interpret, for several reasons. (i) As Candland & Nagy have shown, different species respond to the open field quite differently. For example, if the animals are run for only a few minutes on each of several successive days, the number of fecal pellets left by rats declines; this has been regarded as an index of diminishing "emotionality" (or "fear") with increasing familiarity. But mice display an opposite pattern [136]. (ii) Tobach & Schneirla, too, have studied rats and mice in the open field, but their important findings concern ontogeny: early conditions of rearing, they find, can determine whether the disturbance of exposure to the open field leads to an increase or a decrease in defecation rate [680]. (iii) A number of authors find a lack of correlation among different measures, such as defecation, activity and heart rate [7, 23, 137, 517]. Consequently, the technique has only a minor usefulness at best. If it is used, the term "emotionality" should be avoided for at least two reasons: (i) its use suggests untestable hypotheses about the animal's feelings; (ii) the implication of a single central process underlying all the behavior observed is not justifiable.

10.2.2 The Conditional Emotional Response

A second measure is the "conditioned emotional response" (CER) of Estes & Skinner, described in a paper entitled "Some quantitative properties of anxiety": the CER is defined as "suppression of on-going operant behavior in the presence of a warning signal (CS) which has preceded shock (US)" [225]. As we know, shock can lead to a habit of avoidance, but it can perhaps also have a general effect on behavior (§ 8.3.3). Kimble [364] and Bolles [100] should be consulted for full accounts. An example is given by H. F. Hunt & Brady: they trained rats to press a bar in response to a sound (the conditional stimulus, or CS). They then showed that bar-pressing could be inhibited by shock, even when the shock was not contingent on any action performed by the rats [340]. As illustrated in the title of the paper by Estes & Skinner, the inhibition has been regarded as a measure of the internal state of the shocked animals.

10.2.3 Physiological Changes

The behavior described above is certainly accompanied by quite specific internal changes; but these, unfortunately, are often measured separately by observers who do not describe what their animals do. An exception is Kaada

[349]. His review, and one by Hilton, entitled "Emotion" [323], should be consulted for detailed accounts. We begin with a syndrome, the defense reaction, which has been studied mainly in cats; it has been equated with fear and rage, in the fashion set by Cannon in 1915. It is observed in social situations, not during predation. The cat draws back its head, crouches, flattens its ears and growls or hisses; the hair is raised and the pupils are dilated. "Attack" may follow: the animal runs forward and half-strikes with one or both forepaws; pilo-erection and mydriasis are now often absent. The whole pattern can be induced by electrical stimulation of the posterior region of the hypothalamus, or of the amygdala. An experimenter can thus evoke the behavior at will, and in fully controlled conditions.

The defense reaction is accompanied by extensive cardio-vascular changes: the cardiac output and the contractile force of the heart are raised, and the blood pressure goes up; the vessels of the skeletal musculature dilate, but there is vasoconstriction in the skin and the intestines. The heart rate rises (tachycardia) and the spleen contracts and releases more blood cells. The simultaneous increase in pulse rate and arterial pressure indicate inhibition of the baroceptor reflexes which would ordinarily counter this effect: evidently impulses from the hypothalamus override this homeostatic response. The functional significance of all these changes is perhaps Cannon's mobilizing of the body for exertion in an emergency.

The central nervous processes during the defense reaction are intricately linked with endocrine activity. The hormones especially concerned are those of the adrenal medulla and cortex.

Secretion of the hormones of the adrenal medulla, adrenalin and noradrenalin (sometimes called epinephrine and norepinephrine), has long been known to be increased during various sorts of disturbance. Vogt has described how merely recording the rectal temperature of a rat at first induces an immediate rise in adrenal medullary output [696]. The medullary hormones belong to a group of substances, the catechol amines, of which a third, dopamine, occurs in the brain, especially the limbic system; noradrenalin, too, in addition to being secreted by the adrenal, is present in the brain, especially the hypothalamus. Schildkraut & Kety [582] have reviewed the evidence for a relationship between these "biogenic" amines and behavior. The evidence depends largely on the use of two classes of drugs. Reserpine is an example of the sedative (or tranquilizing) group: its effect on mammals is to reduce activity and responsiveness to stimulation. It also depletes the catechol amines of the brain. The other group of drugs are stimulants. They include amphetamine and imipramine. They induce greater activity and responsiveness, and may counter the effects of reserpine. They also either promote the release of noradrenalin in the brain, or reduce the rate at which it is inactivated by cellular enzymes.

As described in § 5.6.3, the clashes of conspecifics are accompanied by an increased output, or decreased degradation, of the biogenic amines. The defense reaction is also accompanied by release of adrenocorticotrophic hormone (ACTH) by the pituitary gland [323], which stimulates release of steroid hormones by the adrenal cortex (figure 48). While one of the effects of the hormones of the adrenal medulla is to increase the rate of breakdown of hexose, and so to promote release of energy, the function of the adrenal "corticoids" in adverse conditions is less clear. They, too, may contribute to the release of energy; but Wurtman & Axelrod have brought evidence that in addition they interact with the medulla and contribute to the synthesis of adrenalin [725].

The information we have on adrenocortical activity during social interactions is summarized in § 5.6.3. The connection of these changes with the behavior commonly attributed to "emotionality" is in doubt. Ader and his colleagues have presented a critical comment and some negative evidence. They studied albino and hooded laboratory rats, and were unable to find any correlation between the level of one of the principal cortical hormones, corticosterone, in the plasma, and behavioral indices of "emotionality"; nor was there any correlation with adrenal weight [7].

One possible reason for difficulty in relating adrenal cortical activity to behavior is suggested by the work of Stark and his colleagues. They subjected rats to repeated adverse treatments of several kinds, and recorded the response of the system constituted by the hypothalamus, pituitary (hypophysis) and adrenal cortex. Electric shock continued to activate this system even when it was many times repeated: there was little evidence of anything corresponding to habituation or the development of resistance; this was shown by the repeated increase in the level of corticosterone in the plasma after the shocks. By contrast, administration of a number of toxic substances was followed initially by a similar rise in plasma corticosterone, but on repeated treatment this response diminished or was entirely lost. Accordingly, these authors suggest that there are (at least) two mechanisms or pathways by which adrenocortical activity may be evoked; and they show that one pathway, but not the other, may be interrupted by operations affecting one part of the hypothalamus [641–43].

10.2.4. Pathological Changes

Clinical studies, reviewed by Wolff [720], have suggested that exceptional activity of the autonomic and endocrine systems is often linked to pathological changes which can be revealed microscopically. In man these disorders are sometimes called "psychosomatic"; but this term suggests a mind-body (psyche and soma) dualism. Hence a term such as "cerebro-visceral" (which signifies that all the relevant processes are accessible to scientific inquiry) is preferable.

Among the disorders is the development of ulcers in the stomach or duodenum. French and his colleagues have studied the genesis of such ulcers in monkeys (*Macaca*). They induced gastric secretion of hydrochloric acid by stimulating the posterior hypothalamus with implanted electrodes. The peak of secretion then occurred after about three hours, and was due to activation of the pituitary and adrenal cortex. When the stimulation was repeated at four-hour intervals for many weeks, some of the monkeys developed pathological conditions of the stomach, including ulcers [246–47].

This work shows how the system of hypothalamus, pituitary and adrenals can contribute to ulcer formation. The electrode may be regarded as a means of simulating the discharges, presumably from the cerebrum, which can set the whole process going in an intact animal. Further evidence comes from the work of Conger and others. They exposed rats to a conflict situation by administering a shock whenever they approached food: prolonged treatment of this kind led to gastric pathology and sometimes to ulcers [167].

The development of ulcers is influenced by an animal's social environment. This makes a convenient starting point for a further examination of adverse social effects (§ 5.6.3). As we know, social interactions can induce changes resembling those that accompany exposure to a variety of adverse conditions. The changes are adaptive: they tend to enable an animal to survive stressors such as cold and loss of blood. They are injurious only when they go beyond a certain point, as perhaps happens in the social stress described in § 5.6.3.

But social influences on ulceration are not always of this adverse kind: there is evidence also of "social sedation" [46]. Unfortunately, the latter has been reported only among laboratory rats. We have already seen that social isolation may be pathogenic (§ 5.4). In the work by Conger and others, cited above, rats kept in isolation were more likely to develop gastric erosions than those kept in groups. This has been confirmed by Sawrey & Sawrey [575]. Ader has also induced gastric erosions by immobilizing rats for long periods: the resulting gastric pathology was more severe if the rats had also been kept in solitary confinement [3, 4, 6]. The favorable or sedative effects of social interactions require further study.

10.2.5 Death

The final outcome of social intolerance may be death. Among male wild rats in large cages in the laboratory, death is the rule after they have come under repeated attack or threat; sometimes it occurs only after some days, but often within a few hours [37]: it may result from an exposure to attack lasting only ten minutes [227]. The most obviously strange feature of death in these conditions is that it usually occurs in the entire absence of wounding; and severe wounding is not observed. The attacked rats tend to be hyperglycemic, but liver glycogen is low [51]. This, together with the activity of the adrenal cortex, resembles the familiar picture of a mammal responding to an emergency.

Wild rats that die under attack in large cages are in an atypical environment; but it is often difficult to be certain what, in artificial conditions, are the features important for the animal. It might reasonably be supposed that the impossibility of escape is significant. But this should not be taken for granted, for several reasons. (i) The rats do not succumb to being held in the hand, or restrained in a sack, while they are being moved or weighed. (ii) Many rats under attack make no attempt at flight, but repeatedly approach the attacker. (iii) Wild rats have been observed also in quite large enclosures and, in them too, newcomers suffered severe ill effects, evidently from the ostracism they experienced [60, 126]. (iv) Finally, Calhoun has made analogous observations on rats trapped and put in urban areas which already supported a rat population. In the last case, some of the transferred rats emigrated; but many died, despite the opportunity they had to move elsewhere [123]. Nevertheless, none of these observations is conclusive on the importance of confinement: there are too many uncontrolled variables, such as the effects of handling and of transfer to a new environment.

10.3 QUESTIONS ON "DRIVE"

We now return to behavioral analysis, and in particular to the interactions of various sorts of behavior patterns. An animal may be simultaneously stimulated to perform two or more incompatible acts; it may be stimulated to perform an act, yet prevented from doing so; and there are other possibilities. Among a number of questions, we ask whether stimulation to perform A increases or decreases the readiness with which B is performed. Is there evidence of a central drive state, or general arousal [308], which influences all behavior?

This type of problem has been discussed by zoologists under the heading of displacement behavior. The original concept has been reviewed by Tinbergen [679]. An animal, let us say, is performing some stereotyped act, such as mating, but is interrupted by the flight of the partner; on this, the animal turns abruptly to another activity, such as nest-building, eating or grooming. The new behavior *seems* useless and may be performed in an atypical way: it may be hurried or incomplete. This sort of thing may be observed even when animals spontaneously stop an activity. Wild rats, during a series of copulations, may break off for a few seconds, run to food, eat quickly and then resume [37].

There are plenty of such instances, but few detailed, quantitative studies have been made. Other activities by rats, which would certainly have been called displacement behavior as it was originally described, include casual digging or scuffling of loose material; grooming and scratching; and perhaps the hoarding of useless objects, as described in § 4.2.4. A perfunctory brushing of the vibrissae is usually, perhaps always, seen when exploration of an unfamiliar area is temporarily broken off; it also occurs with great regularity when coitus or attack are interrupted.

An important question is whether these and similar performances may usefully be regarded as belonging to a single class. On this, Hinde [326] may be consulted for a wide-ranging critique. A unitary account would be possible if there were common internal causes of the behavior, but at present we know too little of the underlying nervous processes. The most fruitful hypotheses so far relate the behavior to autonomic activity. Stimuli which provoke flight ("fear") also, as we know, increase the activity of the sympathetic nervous system. Relevant experiments have been performed by W. R. Thompson &

Higgins. They put rats at the junction between two compartments of a cage; one compartment was familiar, the other not; some rats were given a shock at the junction. The shocked rats chose the familiar compartment, the unshocked explored the strange area (as one would expect). Rats of both groups displayed what the authors interpret as signs of autonomic activity, namely, face-washing, grooming, scratching and trembling, but these were observed more among the shocked rats [674].

There are other situations in which, more obviously, stimulation to perform one activity increases the readiness or intensity with which another is performed. Barnett and others give an example from the social behavior of wild rats. In experiments in large cages the presence of females increases the intensity of conflict among adult males (§ 5.3.2). Accordingly, it was hypothesized that stimulation to respond with one kind of activity (coitus) increases the vigor with which another (attack) is performed; and that this is not a matter of fighting for females. The hypothesis was tested by observing males, each resident in a large cage, during encounters with strange males: when females were living in the cage, the time spent attacking or threatening the intruders was consistently higher than when females were absent (figures 85, 86). This was true, even though the females took no part in the clashes.

Here is an example of behavior which suggests a description in terms of overflow or of release of tension. Such expressions have been used in the past in discussions of displacement behavior. The behavior has also been described as "irrelevant"; but the attack and threat by the rats in the experiments was relevant to their situation, in that each male was in his territory: a male wild rat does behave intolerantly toward other males in his territory, especially strange ones (§ 5.3.2). Evidently the presence of females lowers the threshold for territorial attack [53]. In this case, then, two kinds of stimulation have an additive effect, expressed in the intensity with which one kind of action is performed.

There is also the possibility that internal deficits can have effects similar to those of external stimulation. Deprivation of water increases the readiness to drink, and of food, to eat; what are the effects of these deficits on other stereotyped activities? The findings for animals in general, which are inconclusive, have been reviewed by Hinde [326]. On rats, there is some indirect evidence. Steiner has studied the effects of deprivation of water: the threshold of arousal, recorded by desynchronization of the EEG, is lowered [648]. Kitai & Morin have recorded a similar consequence of fasting [375]. These changes, detected by electrical means, parallel the familiar restlessness which accompanies deprivation. They do not prove that a fasted rat is more ready, say, to attack a conspecific than is a full one.

With these observations, then, we once again raise the question of general drive: that is, of internal processes which tend to impel an animal to action, though not to any specific action. This concept has been employed by experimental psychologists, such as Hull [339], in describing the effects of such states as food or water deficit on habit formation. A habit is acquired under the influence of food deficit: will the act so acquired be performed under the influence of another deficit, for instance of water? If so, will the strength of the response vary proportionally with the new deficit? In experiments on rats, Webb used as his criterion the number of trials required for extinction of a habit acquired after fasting. Rats deprived of water (but not food) for three hours before testing took nearly twice as many trials to extinction as rats which were not deprived at all; and a further group deprived of water for twenty-two hours took about two and a half as many trials as the controls. Spence has reviewed other, confirmatory observations, and concludes that Hull's "hypothesis of a general drive factor to which any and all acting needs contribute" is supported [635].

An allied question concerns the additive effects of deficits: is response strength a function of the combined deficits of an animal at a given moment? The experimental findings present no simple picture. For instance, Kendler trained fasted rats to press a lever for food; rats which had been deprived of both food and water for twenty-two hours pressed the lever *less* persistently than similar rats which had been deprived only of food for that period. The relationship did not, however, hold for shorter periods of water deprivation combined with the same length of fast [359]. Water shortage interferes with eating (§ 4.4.2). Kendler's work shows further that a simple arithmetical approach to variations in response strength must often be inadequate.

In fact, the phenomena formerly classified in ethology as displacement behavior, and those of experimental psychology covered by such expressions as general drive and arousal, are full of obscurities. What was formerly called displacement behavior is now seen to fall into several categories, none of which corresponds to the original concept [326]. (i) Some activities are held to be the result of the release of inhibition on some pattern which is consequently permitted expression even though the stimulation to perform it is not high. Examples are grooming and preening. (ii) Other performances are evidently by-products of stimulation; for instance, they may be incidental consequences of increased autonomic activity. (iii) It has still to be decided whether a third category is required, of activities evoked as a result of some general central facilitation.

10.4 EXPERIMENTAL NEUROSIS

One of the circumstances in which displacement behavior has been said to occur is when two incompatible activities are simultaneously provoked. The behavior of birds and fish, at least, can sometimes be interpreted in terms of a conflict of drives. Simultaneous stimulation to perform two incompatible acts does not, of course, always lead to the appearance of a third activity: there may be vacillation, or ambivalent behavior. A male wild rat in its territory, faced with a strange male, may oscillate between attack and peaceable approach [37].

The experimental study of animals in conflict situations began with Pavlov. The whole field has been reviewed by Broadhurst [108]. Pavlov was concerned, not with stereotyped behavior, but as usual with the development of new habits. A CR may be set up to a stimulus such as an oval patch of light. An animal so trained may also be trained *not* to respond to another, rather similar stimulus, such as a circular patch of light. In later trials the difference between the two conditional stimuli is reduced, until the animal cannot reliably distinguish between them. Eventually, during this process, the behavior of the animal changes: first, as would be expected, mistakes are made; but, later, severe disturbance results: the ability even to make easy discriminations is lost, the animal resists being taken to the laboratory, and it displays other atypical behavior such as refusal of food or excessive activity.

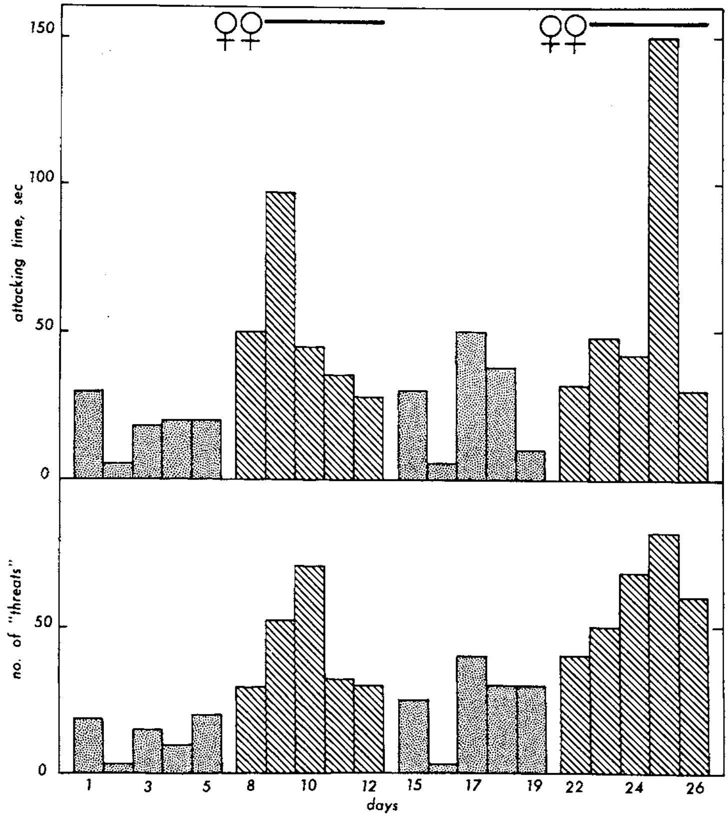


Figure 85. Effect of presence of females on attacking time and incidence of the threat posture (plate 10) by an adult wild male rat. Each rectangle is the record of a single bout, of 15 min, with a strange male. Both attack and threat were higher when females were present in the cage, though they took no part in the encounters. (From Barnett *et al.* [53].)

The name assigned to the whole syndrome is experimental neurosis, but it is uncertain to what extent it parallels any form of disturbed behavior in man. Hebb [306] has examined this question critically. Most of the human conditions labeled "neurotic" are displayed in a much wider range of conditions than is experimental neurosis: the latter is a response to a specific situation in which the animal has repeatedly undergone a confusing experience.

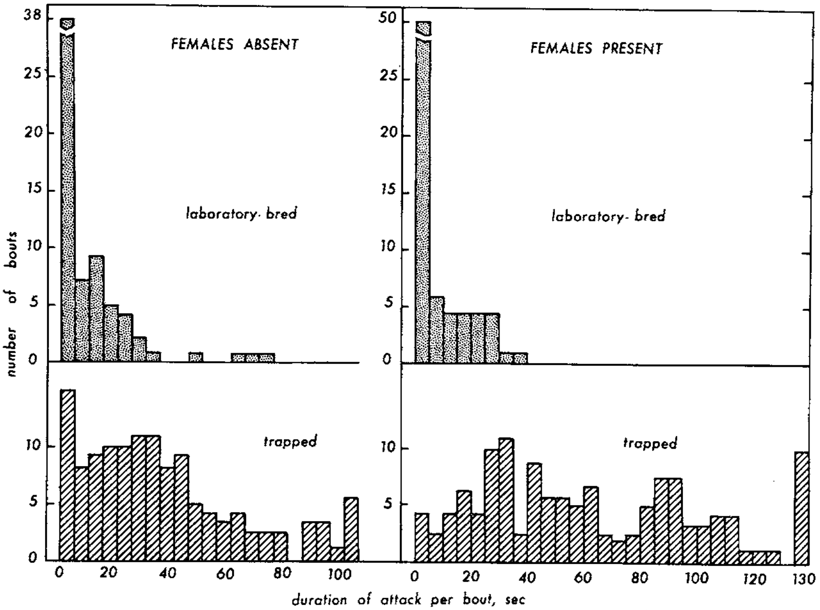


Figure 86. Effects of presence of females on attack by a series of adult male wild rats (compare figure 85). Some had been bred in the laboratory for six to nine generations (upper histogram), some had been trapped. The trapped rats attacked more; and only they were affected by the presence of females. (From Barnett *et al.* [53].)

The conditions in which experimental neurosis develops have been more fully displayed in experiments on trial-and-error (or instrumental conditioning). Cook strapped laboratory rats in a harness and trained them to flex a leg in response to a bright light; he rewarded them with food. If they flexed their leg in the absence of the stimulus they were punished with a slight shock. Once trained, they were further induced to ignore a dim light: if they flexed in response to the dim light they were shocked but, if they did not, the light went out after five seconds. Finally, the intensity of the dim light was gradually raised, so that the discrimination was made more difficult. The rats duly developed disturbed behavior; but the greatest signs of distress were during the two stages before the discrimination was made more difficult, that is, when the leg flexions performed at the wrong time were punished [168]. In this kind of experiment we find, then, an upset primarily due to a noxious stimulus in conditions from which the animal cannot escape. A major resemblance to the Pavlovian situation lies, in fact, in the confinement in harness.

Wolpe has suggested that disturbed behavior is usually due to one of two kinds of stimuli applied *in confined conditions*: (i) aversive stimuli such as shock, and (ii) the ambivalent stimuli first studied by Pavlov. Ambivalence can be produced in three ways. (*a*) It may be due to making a discrimination difficult. (*b*) It may result from increasing the delay before the reward is given: during the interval between the application of the conditional stimulus and the reward, a major effort of inhibition may be required. (*c*) Finally, in some experiments, it is produced by rapid alternation of stimuli which tend to evoke opposite responses [721].

How confinement exerts its ill effects is not certain. It is easy to feel sympathetic to an animal in such experiments, and to reflect that a man too would become exceedingly disturbed in similar conditions. Wolpe suggests that restriction of movement could act in three ways: (i) preventing escape may result in a cumulative action of stimuli which cause anxiety; (ii) anxiety may become associated with the surroundings in which the experiments are carried out; (iii) autonomic responses may become stronger in the absence of the outlet provided by activity of the skeletal muscles. The last suggestion is supported by the work of Anderson & Liddell [17, 413] on sheep (*Ovis*).

Confinement is, however, not essential for the production of experimental neurosis. This has emerged from studies of conflict situations in which the animal is free to move about. In most such situations, admittedly, no disturbed behavior results. N. E. Miller has given a general review [459], and, as he shows, much of the behavior is of a kind easily predictable by common sense. The mythical ass starved to death when equidistant between two equally tempting bundles of hay; but, in fact, an animal faced with alternative goals, both attractive, quickly chooses one. By contrast, if it is between two dangers, and there is no third path for escape, it vacillates at the point equidistant between them. (It is not only cows, *Vaca*, that vacillate—or goats, *Capra*, that are capricious.)

The most notable effect is when a single place or action is made both attractive and a source of pain. Masserman [441] exposed cats (*Felis*) to such a situation and produced typical experimental neurosis. He writes:

Masserman, the cat man,
Makes felines neurotic.
Are cats and humans
Truly asymptotic?

His procedure was to signal the presentation of food, for instance with a light, but to present with the food a strong puff of air which would ordinarily be a severe deterrent. Among the effects were not only disturbed behavior but also internal changes of the sort which accompany anxiety in man.

Corson has given a more detailed account of the physiology of experimental neurosis. His intention is to provide a "biological model of anxiety and frustration": he too emphasises the ill effects of insoluble problems. His dogs, like Pavlov's, displayed marked individual variation: only some responded to treatment with a complete set of pathological signs. These developed a persistent anti-diuresis in the experimental situation, as well as salivation, tachycardia and hyperpnea, despite the fact that they were allowed much more freedom of movement than Pavlov's dogs. The signs continued even when no abnormal behavior could be detected [171].

All such responses seem at first sight to be maladaptive. That is no doubt why they are labeled neurotic, pathological and so on. But, as we can see from the work of Maier on behavior fixations, this is only an assumption. Laboratory rats were faced with an insoluble problem in a Lashley jumping apparatus (figure 7). Whatever solution they chose, they were punished at random, on half their jumps on the average. They were forced to jump by a blast of air (now realized to be an aversive stimulus). The rats tended to develop a fixed response, such as jumping always to the right: indeed, they persisted with their fixated behavior even when the situation was changed, for instance if the door were opened and food made visible on the left-hand side. Once a fixation had developed, the rats were less resistant to making the jump [427]. The detailed interpretation of this study is uncertain, as R. W. Russell & Pretty [571] have shown. A fixation may be regarded as an adaptive response to a situation in which the main result has come to be, not the attainment of the food behind one of the doors, but avoiding the aversive stimulus.

10.5 SUMMING UP

Topics usually discussed under the heading of motivation are referred to in every chapter of this book. A brief summary of the whole subject is now due.

1. In a constant environment, an animal displays changes in the ease with which stereotyped forms of behavior can be evoked. Similarly, fluctuations of internal state influence both the rate at which habits can be acquired and the readiness with which habitual acts are performed. Further, great persistence may be shown in achieving a consummatory state, such as a full stomach, with its consequent ending of internal stimuli which provoked the initial activity. These features of behavior are often termed drive phenomena; they come under the conventional heading of motivation.

2. The internal states and external agencies which make an animal active are usually related, directly or indirectly, (i) to the maintenance of steady states in the individual (that is, they influence homeostasis), or (ii) to reproduction. This is to be expected. The behavior of members of any species, like their other features, is a product of natural selection; accordingly, as a rule it has survival value.

3. Nevertheless, not all activities are directly and immediately related to survival or reproduction. (i) Some are vigorously performed even though of no immediate use. An example is exploration. The value of such behavior for the adult depends on subsequent need for topographical knowledge; for the young animal, exploration is also important in the development of the ability to form habits. (ii) Some activities that are only preliminary to the performance of a directly useful act have reward value: that is, their performance may reduce the readiness with which a stereotyped sequence (such as courtship) is evoked; or they may provide reinforcement. An example is coitus without ejaculation. (iii) An animal put experimentally in an entirely unnatural situation, such as one in which it can stimulate its brain by pressing

a lever, cannot be expected to behave homeostatically, for its ancestors have not been subjected to natural selection in such situations and so have no equipment to deal with them adaptively.

4. Much of the analysis of drive depends on physiology. The best example at present is feeding behavior (§ 4.4). The internal factors involved in feeding which influence the nervous system include, among others, the composition of the blood, the degree to which the stomach wall is distended and impulses from the sense organs of the mouth and pharynx. In the brain, the cortex and thalamus, the hypothalamus (with its centers for both hunger and satiety) and the reticular formation must all play a part.

Just as there is a multiplicity of mechanisms determining the intensity, character and cessation of feeding, so there is sometimes a lack of correlation among different components of feeding behavior: food-seeking activity, for instance, does not necessarily alter in parallel with actual eating (§ 4.4.3.4). Such conclusions apply quite generally: they can be readily exemplified also from reproductive behavior (chapter 6).

5. When a situation requires a vigorous response (attack, flight, coitus) the somatic output is accompanied by marked changes in the autonomic nervous system and endocrine organs (especially the pituitary and the adrenal medulla and cortex); such changes help to maintain the body when heavy demands are put on it. The whole constellation of visible changes constitutes the "expression of the emotions"; but the term "emotion" has many meanings, reflected in the various indices which are said to measure "emotion". The indices include (i) defecation in a strange environment; (ii) disruption of a habit (the CER); (iii) changes of heart rate or of the secretion of various hormones, pathological changes in the gut, and other phenomena—including death.

6. Maximum ability to withstand hostile conditions (stressors) probably requires exposure to mild noxious stimulation in early life. The full development of ability to adapt behavior to experience certainly requires early exposure to a complex environment. These are examples of the importance of sensitive periods in ontogeny: during such periods, the ability to develop certain kinds of behavior is at a maximum; if the appropriate external conditions are absent at the critical time, the result may be a permanent behavioral deficiency.

7. Sometimes, under intense or confusing stimulation, an animal's conduct seems to be ill-directed or positively disadvantageous. This applies both to displacement behavior and to experimental neurosis. Both terms have been applied to heterogeneous categories of behavior. (i) Sometimes, seemingly abnormal behavior is in fact adaptive, as when a behavior fixation enables an animal to avoid pain, or when a so-called displacement act functions as a social signal. (ii) An activity, apparently futile, may be a by-product of a useful physiological process, such as autonomic activation. (iii) There remains an enigmatic group of phenomena in which stimuli which usually evoke one activity seem to lead instead to the performance of another; the second activity can be of varying degrees of relevance to the animal's circumstances.

Perhaps this group will eventually be explained in terms of release of inhibition or facilitation in the central nervous system.

8. The capacity for performing activities beyond those demanded by the immediate situation may confer a long-term advantage on a species. Exploration can be a source of behavioral preadaptation to new conditions.

9. The phenomena discussed above have a plural physiological basis; but there is still the possibility of some form of general drive: that is, central nervous processes which influence an animal's net level of activity, regardless of the particular form that the activity takes. The facts of interaction between one activity and another, found both in stereotyped behavior and in learned habits, have suggested this hypothesis. The concept of general drive has also been related to the rôle of the reticular activating system of the brain stem in maintaining arousal through general facilitation in the cerebral cortex.

Variation and Behavior

11

Dunkett found all his traps fail one after another, and was in such despair at the way the corn got eaten that he resolved to invent a rat-trap. He began by putting himself as nearly as possible in the rat's place.

"Is there anything," he asked himself, "in which, if I were a rat, I should have such complete confidence that I could not suspect it without suspecting everything in the world and being unable henceforth to move fearlessly in any direction?"

He pondered for a while and had no answer, till one night the room seemed to become full of light, and he heard a voice from Heaven saying, "Drain-pipes."

Then he saw his way. To suspect a common drain-pipe would be to cease to be a rat.

Samuel Butler

11.1 INTRODUCTION

In every natural population of a single species there is much genetical variation [442]. Commonly, this is concealed by phenotypic uniformity: for example, small mammals usually have brownish hair above and lighter bellies; yet breeding from rare color varieties reveals a wealth of possible coat colors. In most conditions, and certainly in a typical laboratory, the differences of color are genetically determined. As Haldane has remarked, the concept of natural selection contains a paradox. In a constant environment, natural selection tends to prevent phenotypic change rather than induce it. Individuals which depart from the typical are usually at a disadvantage [282]. If disadvantageous differences from the wild type are genetically determined, the accompanying genotypes tend to be eliminated.

Uniformity is especially important in social communication. To be effective, a social signal, such as a posture, a sound or an odor, must induce a specific response in a member of the signaler's species; often it needs to be readily distinguishable from the signals of other species (§5.6.1). Nevertheless, there is genetical variation which influences behavioral traits, and we must now examine with some care what may properly be said about it.

In doing so, we are concerned with what is sometimes called behavior genetics. There is as much or as little justification for this expression as for the phrase structure genetics. The laws concerning variation, in Darwin's expression, are the same for all categories of traits, behavioral, structural and chemical. The requirements of research and analysis in the genetics of behavior are the same as those for any characters which vary continuously, and which therefore cannot be described in terms of simple Mendelian ratios. They have been fully expounded by Falconer [230] and, with special reference to behavior, in a symposium edited by Hirsch [327]. For a short introductory text, consult Parsons [520].

11.2 EFFECTS OF SELECTION

There are several means by which genetically determined differences may be unequivocally revealed. One is to cross individuals with contrasted characteristics. When the features studied are behavioral, the offspring often resemble one of the two parental types; sometimes they are intermediate. Further breeding, either by back-crossing to one of the parental types or by mating among the F_1 generation, rarely presents a simple Mendelian situation. Behavioral features are usually polygenic: that is, the genetical variation they display is a result of differences at many chromosome loci.

A second method is to select from a mixed population over a number of generations. Tryon began with 142 genetically heterogeneous laboratory rats and selected from them, over eight generations, for two opposite features which he called maze-brightness and maze-dullness. In each generation, the animals were tested in a standard maze, in the dark. One line was selected for the ability to make few errors, the other, for a tendency to make many errors. In this way, two strains were produced, one quick to learn the task, the other slow (figure 87).

Another example of selection for ability to develop a habit has been described by Bignami. His rats were trained in a shuttle box (§7.2.1.4); they were required to take a simple action to avoid a slight electric shock. On the line selected for efficiency in developing this habit, there was marked improvement over four generations; in the opposite line some decline was observed [92].

A third example may be taken from the work of Broadhurst. He was concerned with the quality sometimes named emotionality (§10.2.1). The phenomenon he actually recorded was defecation rate during brief exposures in a strange, featureless environment (an open field). Like Bignami, he bred from a genetically mixed stock of albino rats: by the fourth generation the line selected for low defecation rate hardly defecated at all in the experimental situation; this line is described as non-reactive. The rats selected for a high defecation rate changed rather less [109].

The findings from these experiments give an appearance of simplicity which is deceptive. We must now ask (i) just what has been selected, and (ii) to what extent the observed differences between opposite lines are genetically determined.

On the first question, there is much to be said about Tryon's rats. The terms "maze-bright" and "maze-dull" were doubtless designed to be purely descriptive. Certainly, they avoid the implications of "intelligent" and "stupid"; nevertheless, Tryon's terminology was misleading. Krechevsky gave descendants of the two stocks more detailed tests: the "dull" rats were found to use visual cues more than the "bright" ones [381]. Later still, Searle found the "bright" group to be more influenced by food reward and less distractible than the others. In his experiments, mazes of a different type from those of Tryon were used, and the "bright" rats did not always perform better [596]. Long afterwards, Markowitz & Becker tested rather remote descendants of the original stocks: the animals were required to use visual cues in finding and then re-discovering the way through a maze; in the second part of the experiment, in which the original habit had to be reversed, the formerly "dull" animals performed better than the "bright" [435].

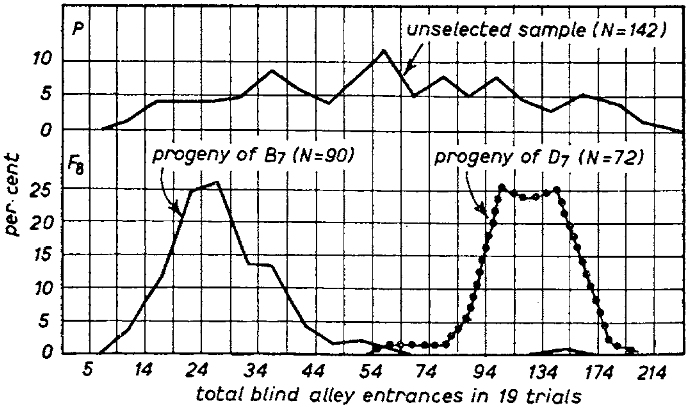


Figure 87. Selection for intelligence. The top graph shows the distribution of intelligence, measured by the number of mistakes made in a maze, among 142 rats in a mixed stock. From this stock selective breeding was carried out for "maze-brightness" (B) on one line and for "maze-dullness" (D) on the other. The result is shown in the two lower distribution curves. (After Tryon [685].)

In general, the maze-learning ability of rats, like the "intelligence" of man, has diverse components. The performance of the rats depends on the kind of stimuli involved. As discussed further below, the environment must be held constant if genetically determined differences are to be established. Further, the words "bright" and "dull" constitute an example of a common difficulty: we try to give up ambiguous terms, such as "learning" and "intelligence"; but we are obliged to use other terms, and, unless we confine ourselves to describing the actual operations performed in our experiments, there is always danger of implying more than we intend.

The second question, on the extent to which the observed differences are genetical, is deferred to §11.4.

The most striking effects of selection in the laboratory are those of domestication, described in §5.4. Genetical change is unavoidable when a species is brought into captivity, if only because not all individuals are fertile in the new conditions. The exact character of the genetically determined changes in behavior, from generation to generation, in a population of laboratory rodents, has not been analyzed in detail. As always, any such study would encounter difficulties in distinguishing genetical effects from those of the environment. Living in a cage itself alters behavior. Moreover, a cage-reared female may produce an environment for her young different from the one she would offer if she had grown up in natural conditions.

11.3 Heterosis

In experimental studies of behavior, genetical variation is often a nuisance. But, while the conventional use of inbred strains, separated from the wild type by tens of generations of rigorous inbreeding, ensures a high level of genetical uniformity, it exacts certain penalties: (i) there is often loss of fertility, that is, inbreeding decline (but the types most used are inevitably those in which this is not serious); (ii) inbreeding may result in excessive phenotypic instability. Inbreeding decline is the obverse of heterosis, or hybrid vigor, defined as superior fitness due to heterozygosis. This is a familiar phenomenon among laboratory rodents: it is easily observed when the many highly inbred strains of mice are crossed [119]. The F_1 mice so produced are usually more fertile than either parent strain. They may also be more active, in some clearly defined sense, or quicker to respond to a change in their surroundings [57, 620].

A less familiar consequence of heterozygosis is reduced phenotypic variation. A hybrid produced by crossing two inbred strains is just as homogeneous genetically as the parents. But, as Lerner [410] has shown, it is often more stable in development than its parents: evidently, the F_1 hybrid is less easily thrown off course in ontogeny by minor environmental fluctuations. It is therefore more uniform in many measurable features. Such a hybrid is particularly suitable for experiments. Behavioral features often vary to an inconvenient extent within an apparently homogeneous population of laboratory animals; hence it is surprising that so many experimenters still fail to use F_1 hybrids. Variation is not always reduced by this means: each instance has to be treated on its merits; but there is no good evidence that heterozygosis ever *increases* variation.

11.4 Components of Variance

Although wild rats certainly differ genetically from laboratory rats, the phenotypic differences we observe may not be purely genetical. They may be, at least in part, due to differences in environment, that is, in the external influences that act on the individual from fertilization on. Similarities between members of a population are often a result, not only of the possession of genes in common, but also of sharing a common environment (including the uterine environment). As an example, laboratory rats of an apparently tame stock may behave in a very intractable way if they are allowed to run free for a time. The obverse also holds: wild rats can be tamed by regular handling from an early age [47]. "Wildness" of behavior may be defined as tending to flee from an experimenter, while "savageness" signifies struggling, biting and squealing when handled. Wildness and savageness, or their opposites, tameness and docility, can evidently be influenced by simple environmental changes.

Strictly, we can be confident that differences in wildness are influenced by differences of genotype only if the animals that differ have been reared in identical conditions. Stone and his colleagues reared wild and laboratory rats, and the offspring of crosses between them, in identical conditions from the time of weaning: the wild rats were, as expected, the wildest in behavior, the laboratory rats were tame, and the hybrids intermediate [656]. To distinguish the part played by genetical differences, it would be more satisfactory to exchange some of the young of pairs of females, one wild and one tame, at birth; some "wild" young would then be reared by a tame foster-mother, and some "tame" young by a wild one. The young that had not been transferred would be controls. But even this design is imperfect: to make the environment uniform from fertilization, newly fertilized eggs should be exchanged between the two kinds of female. No doubt it is unlikely that uterine conditions differ between varieties in such a way that they influence wildness differentially. Nevertheless, as we see below, pre-natal influences on the development of behavior can be detected. Wild and laboratory rats undoubtedly differ genetically in regard to behavioral traits, as they do in hair color and much else; but there is much still to be learned about the environmental influences on wildness, especially in early life.

We must now turn to examples of rigorous experiments. Despite the many difficulties, in the laboratory the genotype can sometimes be held nearly constant, while the environment is varied; or the environment may be held steady, so that the unobscured effects of genetical variation may be studied. Cooper & Zubeck used laboratory rats of the "maze-bright" and "maze-dull" strains already mentioned. They reared some members of both strains in wire cages of which each contained only a food box and a source of water; this constituted a restricted environment. When these rats were tested as adults for ability to find the way through simple mazes, the performance of the "bright" rats was rather poor, and resembled that of the others. The performance of the "dull" rats was unaffected by the boring environment. Other rats of the two strains were reared in cages which provided an "enriched" environment: the cages contained "ramps, mirrors, swings, polished walls, marbles, barriers, slides, tunnels, bells, teeter-totters, and springboards, in addition to food boxes and water pans." In these conditions the "bright" rats did no better than in an ordinary laboratory environment; but the performance of the "dull" rats was now much improved.

These remarkable findings do not show just what aspects of the early environments and the test situations were important; but, as the authors say, the two environments had "differential effects on the learning abilities of bright and of dull rats" [170]. Moreover, they illustrate how we should think of the causes of the differences we observe in any continuously varying feature. If we are concerned with behavior, we may be interested in habit formation, in the intensity of maternal care, in responsiveness to novel stimulation or in other features. The development of each characteristic is influenced by both the environment and the genome; in any population both vary, and so the phenotypic variation of each feature reflects the combined actions of these two sources of diversity. Accordingly, quantitative analysis of the causes of variation demands a statement of the genetical and environmental components of the variance of the character studied [230, 549].

Such an analysis is not simple. As an example, we may refer again to the work of Bignami on rats selected (i) for rapid learning to avoid a shock, or (ii) for slow learning. Reciprocal crosses were made between the two types: that is, "low" females were mated to "high" males, and "high" females to "low" males. Since the two hybrid populations so produced must be the same genetically, they might be expected to be phenotypically identical. But the expectation is based on a concealed assumption: that the environments provided by the two kinds of mother are identical, or at least that they do not have different effects on the characters studied. In fact, Bignami found evidence of a maternal effect: the offspring of the females of the "low avoidance" strain tended to make more avoidance responses, when tested, than the offspring of females of the other type. Bignami also cross-fostered between the two types, but then found no maternal effect. Hence, the maternal influence must have been exerted *in utero* [92]. This work illustrates an important principle: the performance of a mammal reflects its own genotype and consequently that of its parents; but its mother's genotype may also exert an indirect effect, through the environment she provides both before birth and also during lactation. Only rigorous experiment can, in any one example, determine whether observed variation is due to this cause.

11.5 NATURAL SELECTION AND "LAMARCKISM"

Experiments on the effects of selection in the laboratory may be regarded as illustrating, on a miniature scale, the process of evolution. Natural selection requires that a population of a given species be genetically diverse. In nature diversity is always present; moreover, there are mechanisms which tend to maintain genetical heterogeneity [280]. Natural selection requires genetically determined differences in fertility or survival, that is, in the capacity to leave descendants. In addition, the commonest type of individual in a population must be at a disadvantage compared with some rarer type. For if the commonest type were also the fittest, then natural selection would merely act to preserve uniformity, and no change need take place.

Evolutionary modification may therefore be expected when a species, in a part or the whole of its range, is subjected to an environmental change; in a new environment, formerly rare and unsuccessful genetical types may become successful and therefore common. This process takes place over a number of generations, and requires a gradual alteration, in the whole population, of the proportion of certain genes present.

The effects of this process, over periods measured in millions of years, are recorded in the fossil histories of some groups; but the fossil record tells us principally about structure, very little—and nothing detailed—about behavior. Statements are sometimes made about the evolution of the behavior of various forms (including man); but they cannot be tested, and so have not the same status as propositions on the physiology or ontogeny of behavior based on experimental evidence. With more knowledge, it might be possible to suggest relationships between the species of rodents, based on detailed descriptions of their behavior instead of (as at present) structure. But as yet such a comparative account is graveled for lack of matter.

One evolutionary theory has, however, been tested in a study of behavior. McDougall, in a notorious investigation, trained rats to escape from a water tank in which they were obliged to swim to an escape route. There were two ways out: one was a brightly lit alley, but entry into this was punished by an electric shock; the safe way out was dimly lit. Successive generations of rats were so trained, and a progressive improvement in ability to perform the task followed. It seemed that the "Lamarckian" transmission of "acquired characters" had been experimentally demonstrated [446]. Such a process, in which a memory seems to be inherited, is in contrast to the "Darwinian" assumption on the relationship between individual experience and the genetical properties of the individual's offspring.

A controversy of some violence arose, and McDougall's experiments were heavily criticized. One of his errors was a failure to run a control group. Some of the rats in each generation should have been kept untrained; had he found an improvement in this group also, no effect would have been attributable to the training. Munn [490] gives a more detailed critique. Agar and his colleagues later provided not only criticism but also experimental evidence. They bred rats for twenty years, and trained them, in a manner similar to that of McDougall, for fifty generations. Again the rats showed a progressive improvement with time, at least during the first ten years. But a control group also improved during that period; later, both groups declined in performance, and then improved once again (figure 88). These fluctuations, which have important implications for all experiments involving the study of an animal stock for many generations, are attributed to uncontrolled environmental, especially dietary, variations. The detailed reports of this research, maintained with such tenacity through two decades of depression and world war, show that the processes involved in this kind of habit formation are exceedingly complex; they are well worth careful study in the original [13].

11.6 SYNTHESIS

Within a species, variation in behavior, like variation in structure, has both an environmental and a genetical component: the environmental sources of variation include the external agencies which influence habit formation and other changes attributed to "learning"; the genetical component may be analyzed by crossing different types, or by selection, over several generations, from a genetically mixed stock. Domestication always involves selection, even if it is unintentional.

If genetically determined effects are to be studied, it is necessary to control for environmental sources of variation: ideally, all individuals should be reared from fertilization in identical environments. Mammals present special difficulties in this regard: the early environment, uterine and postnatal, is influenced both by (i) the mother's immediate environment, (ii) her early environment, (iii) her genotype. Analysis of their interactions with the genotype of the young is only in its early stages.

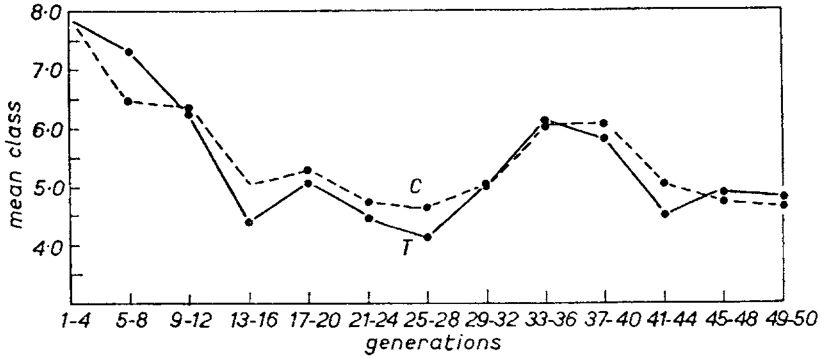


Figure 88. Test for "Lamarckian" transmission. The curves represent mean ability in swimming a maze, by generation. The continuous line refers to rats whose parents had been trained in the maze, the broken line to control rats with untrained ancestors. Both lines show an improvement at first, indicating that the change cannot be attributed to the inheritance of acquired characters. (After Agar *et al.* [13].)

Most animals display a repertoire of patterns of movement which are typical of their whole species or other taxon; the lack of variation in the patterns makes them highly predictable. They are not sharply distinct from reflexes; but those most studied are much more complex and include many reflexes as components of the whole.

Complex action patterns sometimes differ from reflexes because the readiness with which they can be evoked varies: the threshold is lowered with the length of the interval since the act was last performed. The performance of a fixed action pattern thus depends on a fluctuating internal state, as well as external stimulation. Often, an internal state induces generalized movements (§3.2.1.2); such movements occur in the absence of a specific object such as food, or of a particular kind of situation such as that provided by a nest; they end when a specific condition (a consummatory state) is achieved.

The two preceding generalizations do not apply to all stereotyped behavior. There is no evidence that, if rats are deprived of the opportunity to threaten or to attack, they develop an increased readiness to perform these actions. Attack occurs only in response to a particular kind of situation, one which is not in any sense sought. A group of siblings lives together indefinitely without conflict.

Fixed action patterns are usually evoked by standard forms of stimulation (a releasing stimulus), such as an odor, a visual pattern, a sound pattern or a combination of stimuli affecting more than one sense. But here again there are exceptions: eating by no means depends on a single stimulus pattern (§§4.2, 4.3); further, the stimuli which do evoke feeding are determined in part by individual experience. Moreover, the response to a pattern, visual or auditory, is to some extent generalized: the different appearances of an object may all evoke a response, as does a given sound pattern even when presented in diverse forms; this is one way in which an animal adapts its behavior to experience.

Non-specific features of the animal's surroundings may also influence the performance of fixed action patterns. For example, an adult male rat usually attacks other males only in a familiar area.

The standard nature of some behavior patterns has led to the notion that they are "innate" or "genetically coded"; but these terms (unless they merely mean "stereotyped") are inappropriate. The question to ask is: How does the behavior develop? The answer turns out to vary widely, even among the few examples which have been thoroughly studied. Several classes of agents act on the development of behavior and each can influence different features of behavior in different ways. The following list is based on one given by Hebb [310].

(*a*) Genetical: all the factors present at fertilization.
(*b*) Prenatal: the effects of the uterine environment on later behavior have been little discussed in this book; the most obviously likely sorts of effects are nutritional, endocrine or toxic.
(*c*) Postnatal chemical effects—again, nutritional or toxic.
(*d*) Inevitable sensory effects: all the kinds of experience that every member of a species must have in natural conditions, such as those (in a mammal) that accompany feeding in infancy; they can be interfered with experimentally.
(*e*) Variable sensory effects: these are special to the individual.
(*f*) Injurious: wounding, infection and other stressors.

The extent to which a particular sort of behavior is stable or labile depends predominantly on the extent to which it is influenced by agencies of classes (*d*) and (*e*).

No single scheme can accommodate the variety of the fixed action patterns even of a single species. This is not surprising: stereotyped behavior, like everything else about an organism, is a product of natural selection. Genetical variation in fitness, which enables natural selection to take place, influences every bodily feature and process. Accordingly actions, all of which make an elegant contribution to the survival of the species, may be products of exceedingly diverse bodily processes: they may depend to different degrees on different sorts of sensory input and internal states; and they may be more or less labile in development. There is no simple general description of stereotyped behavior to match the standardization we find in each single pattern.

12 The Search for Explanations

I do not know what I may appear to the world; but to myself I seem to have been only like a boy, playing on the sea shore, and diverting myself, in now and then finding a smoother pebble or a prettier shell than ordinary, whilst the great ocean of truth lay all undiscovered before me.

Isaac Newton

This book is primarily about the principles of the study of behavior, sought and propounded for their own sake. The detached investigation of nature, motivated by disinterested curiosity, is rightly accepted as a worthy pursuit. But it is compatible with awareness of the social rôle of scientists and their researches. The activities of rats are often studied for their possible significance in other fields. Much work on laboratory rats is motivated and endowed for its putative value to human psychology. Knowledge of exploratory behavior, or of the effects of reward and punishment, can suggest hypotheses on the upbringing and education of children. Study of abnormal behavior might similarly contribute to investigations of human psychopathology. Certainly, in another area of applied biology, knowledge of the biology of wild rats has helped to prevent disease and to preserve food.

Accordingly, results of academic inquiry may be presented, not only against a general scientific background, but also in relation to their possible uses. In this way two ends may be achieved: that of introducing a reader to some fragment of the strangeness and complexity of the natural order; and that of showing what use may be made of the little knowledge so far gathered.

Whether concerned with applications or not, one is obliged, while actually investigating animal behavior, to adopt a detached attitude. Whatever use may eventually be made of one's findings, the observations themselves, and the theories proposed, should be free from bias. Bias or set can influence, not only what one observes and how it is interpreted, but also the pattern of research or teaching. Rosenthal has shown how it can even affect the conclusions of students given a laboratory project. His pupils (or subjects) were required to train rats on a **T**-maze to go to the darker-painted of two platforms. Some were told that their rats came from a "maze-bright" stock, others that they were "maze-dull"; but, in fact, all were taken at random from a single source. Nevertheless, the students told they had "bright" rats reported greater success by their animals than that recorded by the other group [559].

The history of behavioral research is full of examples of the effects of set. For many years the exceedingly obvious exploratory propensities of rats were almost ignored: most of the workers on rat behavior were studying habit formation, often within a rigid theoretical framework: exploratory activity, if it was noticed at all, seemed irrelevant or inconvenient. The century had begun with Pavlov's work, in which the experimental conditions almost precluded movement. Such a method turns attention away from overt behavior.

Bertrand Russell once suggested that all careful observations of animal behavior tend to confirm the philosophy of the observer.

> Animals studied by Americans rush about frantically, . . . and at last achieve the desired result by chance. Animals observed by Germans sit still and think, and evolve the solution out of their inner consciousness . . . . the type of problem which a man naturally sets to an animal depends upon his own philosophy [568].

Since 1927, when this rather frivolous passage was published, in the highly acquisitive and competitive society of North America there has been a notable amount of work on hoarding by rats; and students of social behavior have been much occupied with relationships of dominance and subordination. Meanwhile, the study of "instinct" has flowered in the conservative lands of western Europe. This study at first neglected ontogeny and made unwarranted assumptions of rigidity in the development of behavior.

It is reassuring that all these attitudes to research have been fruitful. Certainly, once a topic for study has been chosen, a high standard of rigor in the design of experiments and the interpretation of results has often been achieved. In any case, the divisions of outlook and method between the different schools are now disappearing. Few workers disagree on the need for objectivity, though they do not always adopt the same methods of achieving it. Objectivity, however, should not be made a dogma or a fetish. Subjective or anthropomorphic assertions can lead to useful observations or fruitful hypotheses, though these are often not clearly formulated. They should be avoided, consciously and conscientiously, when they lead to disagreements *which cannot be resolved.* In a pilot study, Barnett & Spencer referred to certain behavior as aggressive [60]. Another observer privately described it as representing fear. No means exists or can be proposed for settling differences of this sort.

The attempt to achieve rigor has led to a meticulous avoidance of subjective expressions which makes some writings on behavior read oddly. (No doubt this book provides many examples.) It may not matter much whether one refers to a "hungry rat" or a "rat which has fasted for twelve hours"; the second phrase is more informative: without the last three words it is equivalent to the first. Subjective or mentalistic phraseology can indeed often be given an objective (operational) meaning. In scientific communication it is not usual to say that an animal "knows" something. Bertrand Russell has remarked on the ambiguity of the word "know" [570]. "Knowing" may conveniently, for some purposes, be defined as "acting appropriately": "This is the sense in which we say that a dog knows his name, or that a carrier pigeon knows the way home" [570]. But even more important than an objective vocabulary is the use of a unitary or monistic way of speaking. There are several examples of the value of this method in the preceding chapters.

Consider the phenomenon of the unexplained death of rats under attack (§10.2.5). If we used the dualistic language colloquially employed for man, we should attribute the condition of the stricken rats to "mental" rather than "physical" causes. In conversation, "shock" or "humiliation" are often suggested. But these expressions have little or no explanatory value. One of the distant aims of the research on social stress is to assign the deaths to measurable processes in the body; death could then perhaps be prevented by interfering with those processes. The methods of physiology are assumed to be capable of revealing the causes of this kind of death. At present it is possible to describe only some of the relevant internal changes, but there are no grounds for assuming any totally new principle or separate mode of being involved in this (or any other) aspect of behavior.

A unitary interpretation need not be physiological. Certain sorts of explanation are expressed in behavioral terms. It may be asked why attack, without wounding, by a conspecific has such a violent effect. A tentative answer may be given by referring to other work. Certain kinds of situation cause flight by mammals of other species. Hebb has described how chimpanzees (*Pan*) are terrified by the stuffed head, without the body, of another chimpanzee: in general, he says, it is frightening to see something which has, like a ghost, only some of the attributes of a familiar object [305]. The avoidance of new objects displayed by wild rats (§3.3) is a similar phenomenon. Perhaps neophobia has a counterpart in the meeting of a newcomer with a resident male. Rats are in general sociable creatures: attack, or at least severe attack, is an anomaly in the lives even of wild rats. It represents, perhaps, a sharp contrast with the norm or the "expected"; and this may induce the ill effects observed in the attacked rats [51]. Whether this tentative hypothesis is or is not valid, the explanation proposed is behavioral and is independent of physiology. It is, of course, less satisfying than a physiological one: physiology enables us (at least in principle) to deduce the properties of a system from its own organization; a generality about behavior may have predictive value, but no more.

The preceding passage implies that correct prediction is desirable. No doubt, few will quarrel with this assumption. In practice, correct prediction is the test of the validity of many, perhaps most, of the general propositions asserted by scientists. It has been called a "metaphysical directive"—which perhaps means no more than Euclid meant by axiom. Another directive, Occam's razor, is usually misquoted as *entia non sunt multiplicanda praeter* *necessitatem.* (Occam actually wrote: *pluralitas non est ponenda sine necessitate.*) These exhortations express a general refusal to assume the existence of more, or more complex, entities than the least and simplest needed to explain the facts. (It might be interesting to make a search for instances in which adherence to this principle has led to error.)

The techniques of observation, experiment and communication used in the study of behavior have been developed in the quest for reliable methods of answering specific questions rigorously stated. "Science consists largely of devices for inventing concepts having a greater degree of precision than is found in the concepts of everyday life" [570]. It is rather rare for a psychologist, for instance, to ask (as a layman may ask), "What is consciousness?" (In the same way, biologists do not often ask, "What is life?") They ask, say, what are the effects of injury to the reticular formation on a measureable feature of behavior [584]. One of the most important elements in recent history has been the growth of methods which enable us to answer such specific questions with a good deal of confidence.

Nevertheless, ethology has also some general principles to offer, though at present they give us only a provisional conceptual framework.

(i) First is the truism that an animal's behavior contributes to the fitness (in the strict, Darwinian sense) of its species. (a) Some behavior does so by being closely linked to homeostatic processes: as a rule, an animal drinks when it needs water, eats when it needs a source of energy and so on: in this way, osmotic relationships, body weight, body temperature and other quantities are kept steady. This entails a complex system of negative feedbacks, operated especially by the nervous system. (b) But reproductive behavior too contributes to fitness, though not to homeostasis: that is, it does not influence steady states on which the animal's life depends (though maternal care is needed for survival of the young of many species). (c) Behavior may contribute to fitness without being directly linked either to homeostatic processes or to reproduction. This holds for exploratory behavior, which (α) gives information which may later be of use (through the accompanying "latent" learning), (β) increases "intelligence" in young animals (by making deutero-learning possible). It also applies to territorial behavior—which usually takes the form of deterrent signals by one animal and withdrawal by another.

(ii) Much behavior, notably that involved in mating, the care of young, defense of territory and the construction of nests and so on, is highly stereotyped and predictable in detail for each species. We consequently speak of fixed action patterns. Most land animals, and many aquatic ones, have species-characteristic behavior patterns or other features which evoke standardized responses in other members of their species. These social signals ensure either (*a*) approach and subsequent mating or parent-young interactions; or (*b*) dispersion. In the past, behavior of this sort has been called "innate" or "instinctive"; but it is now seen to occupy positions in a continuum of acts of which the development ranges from highly labile to relatively fixed.

(iii) One of the notable general features of behavior is its lability: most animals can alter their responses to a given class of stimuli in accordance with their experience of reward or punishment. The internal processes, no doubt very diverse, which underlie this adaptability are often lumped together under the excessively general term "learning"; this term also covers the processes which take place during exploration, imprinting and so on, mentioned in (i) above.

(*a*) The form taken by acquired habits is often determined by the fact that a particular response cancels a deficit. (*b*) The goals which an animal tends to learn to achieve are not constant. There are often autonomous changes (as in breeding cycles) in an animal's internal condition which cause corresponding cycles in behavior. (*c*) A few of the internal states which impel an animal toward specific goals have been partly analyzed. The processes involved are multiple: not all are *directly* homeostatic even when they are concerned with homeostasis; in particular, an activity such as eating or drinking may cease as a result of afferent impulses which are independent of the internal change which initiated eating or food-seeking.

(iv) Habit formation, except in its simplest forms, is not a substitution of one response (or no response) for another: it cannot be described in terms of the classical conditional reflex. It involves (*a*) selection of one set of responses from among many, in trial-and-error behavior; (*b*) processes of generalization and discrimination; and (*c*) "insight behavior" in which separate previous experiences are combined to make a pattern fitted to a new situation.

(v) Behavior varies in the individual in three ways (of which two have been mentioned above): (*a*) there are the fluctuations in internal state; (*b*) there are the adaptive changes of habit formation; (*c*) there are developmental changes. As for the last, sometimes a fixed action pattern can be evoked only when the animal is sexually mature; other patterns appear at birth (or hatching or emergence). Neither the time of their appearance, nor their uniformity, tells us anything conclusive about how they develop. Some fixed patterns develop normally only if the young animal is subjected to specific experiences during an early sensitive (critical) period. Sensitive periods are also important in the development of "intelligence"; the deutero-learning mentioned in (i) above can take place fully only in early life.

(vi) All development involves an interaction of (*a*) the coded information in the genes with (*b*) the animal's environment. Some behavior patterns are not only stereotyped but also exceedingly stable in their development: they seem to appear in virtually any environment which allows the animal to develop. These are the patterns sometimes said, incorrectly, to be innate, or genetically determined. Others are more labile: they depend a great deal on the particular sensory inputs experienced by the individual. Some sensory effects, such as those of a nestling in contact with its mother, are inevitable except in very special experimental conditions. Others are variable and are responsible for most habit formation.

(vii) The central nervous system connects the sense organs to the effectors and is also an organ of adaptation. It selects from the input only certain patterns and organizes the motor output either in species-characteristic or in individually acquired patterns. We do not know how it does this.

It is appropriate to end this summary of principles with a statement of ignorance. Our knowledge of facts is growing quickly, but we have as yet taken only a minute sample of the varieties of behavior to be found in the animal kingdom. There are several rigorous methods of study, each fruitful, including those of field ecologists and neurophysiologists as well as those used in direct observation. A few generalizations, valuable but of small scope, can be made, at least on the plane of overt behavior; but the underlying physiology is baffling, and no grand synthesis is yet in sight. Newton's great ocean of truth remains all undiscovered before us.

Appendix: On Definition

It is just because the terms of science are so well defined, and defined in a way which is closely tied down to the phenomena, that questions in science can be settled: only because this is so can scientists hope to answer definitely the questions that arise for them, by looking to see whether things actually happen in nature in the manner the theory suggests.

Stephen Toulmin

In the writing of this book it has been assumed that precise and consistent definition of technical terms helps in conveying what is meant. This may be regarded as an hypothesis about human behavior. It is, of course, based on the experience of teachers and others. There are successful scientists who dispute, or at least ignore, this view. Some say that words can never match the complexity of events and that semantic rigor is unattainable. The reply to this is that an approximation to rigor is nevertheless possible and useful. Others say that definitions must always be provisional: meanings change as a subject advances. This, however, is not a cogent argument against agreed definitions in a given work.

The word "definition" has itself several meanings, fully discussed by Robinson [551]. For instance, an *ostensive definition* is one in which an object is indicated to an audience and the name to be attached to it is then given. An example is the formal naming of a new species by a taxonomist.

In this book, two other sorts of definition are more important. The first is *lexical definition*. In a dictionary dealing with current usage, the assertions about the meanings of words are historical statements: they purport to tell the reader how words have in fact been used in the recent past (and by implication how they are being used now); they may consequently be true or false. The second is entirely different. It is *stipulative definition*. This is a statement of intention. The writer says, in effect: from now on I shall use this term in this particular way, and you, the reader, are asked so to understand it. This is what Lewis Carroll's Humpty Dumpty had in mind when he said that words meant what he intended them to mean. A stipulative definition cannot be true or false, unless one applies these terms to the writer's success or failure in keeping his word.

It is therefore never admissible for a critic to complain that stipulative definitions are incorrect. Admittedly, such a definition may not conform to current usage (as in the chemists' definition of the term "salt"); and it may for that or other reasons be *inconvenient*. But, it can never properly be said to be *wrong*.

Sometimes a completely new term (such as "conditional-reflex") has to be coined; in such a case—given care in the initial defining—no trouble should follow. The stipulative definitions that one adopts are nevertheless usually based on an accepted convention. The more this is possible, the better. But when common terms are confusing, it may be necessary to disregard them and to ask, What are the facts? and then to try to describe the facts in neutral and unambiguous language. Such description involves a departure from usage which is sometimes very difficult to make. It is the opposite of a procedure often adopted, namely, to accept a term in current use (such as "instinct" or "aggression" or "arousal") and to assume that there must be a class of events that matches it. When this assumption is made, it may lead to some such question as, "What is the essence of instinct?" Looking for "essences" is a wild goose chase: what one needs is actual observations to which one may assign a name. Hence, words such as "instinct" may fall into disuse, as no longer convenient. When this happens, it is still necessary to deal with the facts, concepts or theories subsumed by the rejected term. Precise definition is no substitute for observation, experiment or the formulation of hypotheses, but it can aid in all of them.

Glossary

A lexicographer is, pace *Dr Johnson, something more than a harmless drudge.*

A. J. Ayer

The notes below are primarily designed to state how the terms listed are used *in this book.* "[Not used]" means that the term has been used, if at all, only in a discussion of facts and concepts to which the term is applied by others. In addition to giving stipulative definitions (see Appendix), the entries also constitute *recommendations,* inasmuch as the author has found the usages convenient.

For a comprehensive list of terms and meanings, with caustic comments, see Verplanck [693].

Aggression [not used]. A word with many meanings, and a source of much confusion. § 5.6.2.

Anxiety [not used]. A state, usually aroused by noxious stimulation, in which there is raised autonomic activity. External signs include more-than-usual defecation, producing wet feces, urination and grooming. (*Fear* is the same, but 'fear' is customarily used only if the condition lasts for a short time.) § 8.3.3.3.

Appetitive behavior [not used]. Variable behavior, often impelled by an internal deficit (see homeostasis) and ended by its abolition.

Aversive. Causing withdrawal or avoidance.

Bait-shyness. Refusal of food previously accepted, after eating it has been followed by illness. (Must not be confused with *neophobia,* q.v.)

Commensal. Sharing the same food. In this book, used to distinguish species that depend on man for food.

Conditional reflex (CR). A response, elicited by a previously indifferent stimulus (CS), as a result of repeated application of the CS at about the time of application of a releasing (unconditional) stimulus for a similar act. The response is usually mediated by the autonomic nervous system, but may be a tendon reflex. (This is classical, Pavlovian conditioning, or CR type I.) The CS is "indifferent" only with respect to the activity to be studied: it must arouse attention from the first. § 7.2.2.

Conditioned reflex. See *Conditional reflex.*

Deutero-learning. Development of ability to solve problems during diverse experience in early life. § 8.7.2.2.

Displacement behavior [not used]. § 10.3.

Dominance. Often ambiguous term referring to an animal's having prior access to place, food or a mate (of members of a conspecific group; should be distinguished from an animal's superiority due to being on its own territory). § 5.3.5.

Dominance hierarchy [not used]. See *Status system.*

Drive [not used]. An internal state causing altered activity (often accompanied by an epithet, as in "hunger drive"). §§ 9.3; 10.3.

Emotionality [not used]. § 10.2.

Ethology. The science of animal behavior.

Expectancy. An inferred representation in the central nervous system of a pattern of stimulation which has in the past followed the situation in which the animal now finds itself. § 8.4.

Exploratory behavior. An imprecise term referring to apparently unrewarded movements about an animal's living space. §§ 3.2; 3.4; 8.7.2.2.

Exploratory learning. Inferred storage of information in the brain leading to superior habit formation after apparently unrewarded experience of a situation. § 3.4.1.

Extinction. Decline in performance of a habit as a result of its repeated evocation without subsequent reward. § 8.5.

Fear. See *Anxiety.*

Fixed action pattern. Stereotyped, highly predictable, taxon-specific behavior sequence. (This kind of behavior is still often called "innate" or "instinctive"; but these terms are ambiguous or confusing.) § 9.2.1.

Habit. Pattern of response individually developed.

Habituation. Decline in performance of an act as a result of repetition of a stimulus which evokes the act. (Often reserved for decline in a *stereotyped* act such as a reflex.) See *extinction.* §7.3.2.

Homeostasis. Maintaining a steady internal state.

Imprinting. Development, during an early *sensitive period* (q.v.), of the tendency to follow or otherwise approach an object (usually another animal of the same species). § 8.7.2.1.

Inhibition. Any internal process which prevents or reduces the performance of an action. (In nerve physiology has a different and more specific meaning.)

Inhibition, internal [not used]. Synonym for *extinction* (q.v.).

Innate behavior [not used]. See *Fixed action pattern.*

Innate releasing mechanism (IRM) [not used]. §§ 9.1; 9.2.1.

Insight behavior. A sudden adaptive change in behavior. See *Expectancy, Exploratory learning.* § 7.3.4.2.

Instinct [not used]. § 9.1.

Instrumental conditioning [not used]. See *Trial-and-error behavior.*

Intelligence. Ability to adapt behavior to experience. (Not a useful term, unless the behavior is specified.) § 7.3.4.

Latent learning. Synonym of *exploratory learning* (q.v.).

Learned behavior [not used].

Learning [not used].

Motivation [not used]. See *Drive.* §§ 9.3; 10.3.

Neophilia. Approaching unfamiliar, in preference to familiar, objects or places. § 3.2.3.

Neophobia. The avoidance of unfamiliar objects in a familiar environment. § 3.3.

Operant conditioning [not used]. See *trial-and-error behavior.*

Punishment. A response-contingent *aversive* (q.v.) stimulus. § 8.3.3.

Reinforcement. The operation of a *reward* (q.v.).

Reward. A stimulus which strengthens the response that evokes it. § 8.3.1.

Sensitive period. A period in an animal's life, usually early, when it is especially easy to evoke a particular kind of behavior or to acquire a particular kind of habit. § 8.7.2.

Signal. A small change in distribution of energy or matter which induces a much larger change.

Social facilitation. Increment of behavior due to the presence of a conspecific. A very general term covering a variety of phenomena. §§ 4.2.1.2; 8.2.4.2.

Social signal. A *signal* (q.v.) from a conspecific.

Status system. A group structure based on *dominance* (q.v.) and *subordination* (q.v.).

Stimulus. An event (usually a *signal,* q.v.) which excites any of an animal's receptors.

Subordination. The obverse of *dominance* (q.v.).

Territory. A region occupied (by an individual, pair or group) to the exclusion of other conspecifics. § 5.3.

Threat. A *social signal* (q.v.) which tends to cause withdrawal. §§ 5.2; 5.3.

Trial-and-error behavior. Gradually acquiring a habit; involves an increase in efficiency through elimination of unnecessary movements. (Equivalent to, or includes, CR type II, operant conditioning and instrumental conditioning. It differs from the classical *conditional reflex* [q.v.] in that there is an initial phase of ineffectual movements.) §§ 7.2; 7.3.4; chapter 8.

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(Some of the titles of papers have been shortened. The numbers in parentheses after each entry are those of the pages on which it is mentioned.)

ABBREVIATIONS

AB	*Animal Behaviour*
AJP	*American Journal of Physiology*
BJAB	*British Journal of Animal Behaviour*
CRSB	*Comptes Rendus de la Société de Biologie de Paris*
GPM	*Genetic Psychology Monographs*
JCPP	*Journal of Comparative and Physiological Psychology*
JCP	*Journal of Comparative Psychology*
JEP	*Journal of Experimental Psychology*
JN	*Journal of Nutrition*
PB	*Physiology and Behavior*
PR	*Psychological Review*

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