STUDIES IN ANIMAL BEHAVIOR

S. J. HOLMES

STUDIES IN ANIMAL BEHAVIOR

S. J. HOLMES, Ph.D.
ASSOCIATE PROFESSOR OF ZOOLOGY, UNIVERSITY OF CALIFORNIA

BOSTON: RICHARD G. BADGER
TORONTO: THE COPP, CLARK CO., LIMITED

Made in the United States of America

The Gorham Press, Boston, U.S.A.

PREFACE

THE present volume is largely devoted to subjects with which the writer's own investigations in animal behavior have been more or less closely concerned. For the interest of the general reader the special contributions of the writer have been made subordinate to the broader aspects of these subjects. Although there is little relationship between the various topics dealt with, the different chapters are not devoid of a certain unity of aim. The several types of behavior here described were studied in the endeavor to get a fuller insight into their mechanism, or to interpret them from the genetic point of view. These two methods of attack are not opposed or mutually exclusive, as is sometimes implied, but complementary. We cannot obtain a complete explanation of behavior by an analysis of the activities of the individual alone; it is necessary to know also the evolutionary history of the species, and the various steps by which its present behavior has been acquired.

The first chapter is historical and will, it is hoped, prepare the reader for a better appreciation of the general aim and import of what follows. Some of the chapters in this volume have appeared elsewhere as special articles. I wish to thank Dr. J. McKeen

Cattell for his generous permission to republish chapter VI from *Science*, and chapter XIII and parts of chapter XI from the *Popular Science Monthly*. The Wisconsin Society of Natural History has very kindly allowed me to republish chapter III which originally appeared in the bulletin of that society for June, 1912.

CONTENTS

STUDIES IN ANIMAL BEHAVIOR

STUDIES IN ANIMAL BEHAVIOR

I

ANIMAL PSYCHOLOGY, THE OLD AND THE NEW

PSYCHOLOGY is a science that has had few historians, and the special province of animal psychology has never been accorded the dignity of a full and thorough historical treatment. It is far from the intention of the present writer to take up this neglected task. But there are a few salient features of the development of this branch of the science which it may be desirable to consider briefly in order to prepare us for an appreciation of the aims and methods of present-day animal psychology.

The animal mind has enlisted a certain amount of interest from the earliest times. Do animals have souls? If so, Do these souls continue to live after death? How do the souls of animals differ from the souls of men? Do animals reason?—these are some of the questions which exercised the earliest philosophers, and they have been asked more or less persistently down to the present time. Among comparative psychologists these questions, except perhaps the last, are no longer in the foreground of interest. Professor John Dewey has remarked that in philosophy we do not solve our problems; we get over them. And these old questions about the animal mind that have so long perplexed enquiring spirits we have now gotten over, rather than solved, and left behind in order to turn our attention to more fruitful subjects of investigation.

Modern psychology troubles itself very little about the soul as an object of enquiry, and animal psychology concerns itself with this subject still less. There are a number of questions about consciousness which still occupy us. Where did consciousness begin in the course of evolution, if it can be said to have had a beginning at all? How is consciousness related to the bodily structure of the organism? What are the criteria by which its presence in an organism may be recognized? How does it influence behavior, if we grant that it can influence behavior?—these and many other related problems continue to perplex the scientific worker and the metaphysician alike. But many of the problems are beginning to recede from the foreground of interest, and to a considerable extent we may get over them in the future and leave them to one side, although at some time we may recur to them with renewed insight and find that they wear a quite different aspect.

Even among the ancient Greeks we find much the same diversity of opinion in regard to the mental life of animals that occurs in modern times. While it was contended by some that the animals occupy a position immeasurably below that of man, the Greeks in general were inclined to a more generous estimate of the animal mind. Apparently there were no sustained studies of animal psychology among the ancient Greeks, with the single possible exception of the observations of Aristotle, most of which, however, were of a desultory character. Aristotle's three treatises on zoology contain numerous records of the habits of animals, and his general estimate of the mental powers of animals might well pass for that of a conservative psychologist of the present time. Most animals, according to Aristotle, "appear to exhibit gentleness or ferocity, mildness or cruelty, courage or cowardice, fear or boldness, violence or cunning; and many of them exhibit something like a rational consciousness, as we remarked in speaking of their parts. For they differ from man, and man from animals, in a greater or less degree; for some of these traits are exhibited strongly in man, and others in animals." The animal mind corresponds to the undeveloped human mind, for in speaking of infants Aristotle remarks, "nor does their soul at this period differ in any respect from that of an animal." ("Hist. of Animals," Bk. 8.)

The sage observation that the life of animals "may be divided into two acts, procreation and feeding, for in these two acts all their interests and life concentrate," recalls the aphorism of Schiller that hunger and love are the ruling forces of the world. Aristotle was very far from regarding behavior as determined by external stimulation. He had no conception of reflex action, no knowledge of the function of nerves, and he regarded the brain as an organ to temper the heat of the heart, the latter being considered as the seat of sensation.

The doctrine that animals reason found an ardent defender in Plutarch, who devotes two rather curious chapters of his "Morals" to a consideration of the mental powers of animals and their relation to the faculties of men. Different views are put forward in dialogue form much after the fashion of Plato. The discussions are of interest mainly as presenting the views of animal intelligence current in Plutarch's time. Porphyry's views of animals were much like those of Plutarch, although they were interwoven with his Neo-Platonist doctrines concerning the nature of the soul.

The Romans, like the Greeks, were generally inclined to give credit to the lower animals for a considerable amount of intelligence. Pliny with his usual uncritical judgment related many stories of wonderful animal sagacity, and Celsus contended for the essential similarity of mind in brute and man. Galen shows an approach to the conception of instinct as it came to be understood by later writers. He dwelt at length on the adaptations of the structures of animals to the uses to which they are put, and upon the inborn proclivities of animals for using their parts in the proper way. Just as the muse incites the poet, so do the innate impulses of animals lead them, without instruction, to perform the acts needful for their life. Similar views were expressed in the writings of Cicero, (*De Natura Deorum*). Seneca wrote in much the same vein: "What practice teaches is slowly acquired and is made after many patterns; what nature teaches, that is the same for all, and, as soon as there, it takes place without reflection." "Nature teaches nothing but self-preservation and the knowledge necessary for this end."

During the Christian era there were few recorded observations or speculations on animal psychology before the Renaissance. Interest was centered mainly in man, and especially in things affecting the welfare of his soul, and most of the attention that was bestowed on the mental life of animals was owing chiefly to the bearing of the subject upon theological teachings. The church emphasized the inferiority of the brute creation and taught that it was brought into existence solely for the service of man, although this doctrine was sometimes qualified by the admission that certain noxious creatures might have been produced by the devil, or came into existence as a consequence of the Fall.

The conception of instinct which had assumed more or less definite outlines among Roman authors came to be more clearly defined by the theological writers of the latter part of the Middle Ages. Of these St. Thomas Aquinas stands preeminent as an authority on the animal mind as upon most things else. Aquinas makes a sharp distinction between the sensitive soul (anima sensitiva) and the intellectual soul (anima intellectualis), ascribing the former to brutes, and the latter only to man. Animal and man are therefore separated by a broad and impassable barrier. Animals have sensations, sensory memory, but they have no reason (*Summa Theologica,* LXVI and LXXXIIB), no real freedom (*l. c.* CXIII), no responsibility. "No activity of the sensitive part can have place without a body. But in the souls of dumb animals we find no activity higher than the sensitive part. That animals neither understand nor reason is apparent from this, that all animals of the same species behave alike, as being moved by nature, and not acting on any principle of art; for every swallow makes its nest alike. Therefore there is no activity in the soul in dumb animals that can possibly go on without a body." (*l. c.* LXVI.)

"Sense," he says, "is found in all animals, but animals other than man have no intellect; which is proved by this, that they do not work, like intellectual agents, in diverse and opposite ways, but just as nature moves them to fixed and uniform specific activities." "Sense is cognizant only of singulars, but intellect is cognizant of universals. Sensory knowledge extends only to bodily things, but intellect takes cognizance of things incorporeal, as wisdom, truth and the relations between objects." The wonderful adaptiveness and perfection of instinct are not to be ascribed, in any measure, to the animal's own initiative, but redound to the credit of the Creator.

The ideas of Aquinas on animal psychology, like his ideas on so many other subjects, were greatly influenced by the teachings of Aristotle, but he emphasized much more than his master did the differences between brute and human intelligence. Aristotle greatly perplexed his followers and interpreters by his vague and somewhat vacillating treatment of the relations of the rational soul to the sensitive soul and to the body. But the learned St. Thomas promptly settles these problems with a decisiveness that leaves no room for doubt concerning his own standpoint. The writings of Aquinas served to define the position of the church in regard to the status of the animal mind. The opinions of this prelate were widely followed and have continued to influence opinion even down to the present time.

In the writings of Descartes we find animal behavior interpreted, for the first time, in terms of the functions of the nervous system. Descartes was an original investigator of the structure and functions of the nervous system and he arrived at many of our fundamental conceptions of nerve physiology. His celebrated doctrine that animals are automata, that their activities are entirely determined by their bodily organization without knowledge or will of their own, was simply the result of carrying out to its full logical consequences the mechanistic physiology that he had adopted. "I have diligently enquired," he says, "whether all the motions of animals came from two principles, or only from one; and as I find it clear that they arise from that principle alone which is corporeal and mechanical, I can by no means allow them to have a thinking soul. Nor am I at all hindered in this conclusion, by the cunning and sagacity of foxes and dogs, nor by those actions done from lust, hunger or fear; for I profess to be able easily to explain all these things by the sole conformation of their limbs."

Although Descartes explained by a physical mechanism what had been previously ascribed to the sensitive soul, his conclusion was equally acceptable to most of the dignitaries of the church, inasmuch as it preserved an essential distinction between the brute creation and man. In fact this disposition of the animal world was hailed with satisfaction by many church authorities, and it was rapidly followed by various writers several of whom developed even more extreme views. Malebranche, for instance, tells us that "Among cats and dogs and other animals there is no intelligence, no spiritual soul as we are commonly told. They eat without pleasure, cry without pain. They grow without knowing it; they desire nothing; they know nothing, and if they act with address, and in a manner that indicates intelligence, it is because God, in making them for self-preservation, has constituted their bodies in such a way that they withdraw organically and without knowing it from all that can destroy them and that they seem to fear."

A reaction from such views was inevitable. They incurred the ridicule of La Fontaine, the protests of the good Father Bonjeant, who believed that animals were inhabited by the souls of demons, and the criticism of Thomasius, Gassendi, Leibnitz and many others, of whom the French Inspector of Forests, G. LeRoy, occupies a position of especial prominence. LeRoy's *Lettres sur les Animaux* contain many observations on the training of animals and other indications of intelligence, but their chief distinctive feature is their attempt to explain the actions commonly attributed to instinct as the result of intelligent experience. A more strenuous attempt in the same direction is found in Erasmus Darwin's *Zoonomia.* Darwin argues that the marked resemblance in the form and functions of the bodies of man and animals should lead us to expect a similar endowment of sensations, emotions and mental powers generally. He endeavors to show that the habitual acts of animals are learned like most of our own, and that certain habits appear innate simply because we do not attend with sufficient care to the early stages of their formation. The chick walks soon after hatching, but before this time it moves its feet about while in the shell. It pecks at food, but before this it opens and shuts its mouth and swallows some of the white. The ability of calves and colts to walk soon after birth is attributed to their struggles while still in the uterus. Even the human fœtus sucks in amniotic fluid and "learns to swallow in the same manner as we learn all other animal actions which are attended with consciousness, by the repeated efforts of our muscles under the control of our sensations and volitions."

Breathing, a more difficult case, is accounted for as follows: "The inspiration of air into the lungs is so totally different from that of swallowing a fluid in which we are immersed, that it cannot be acquired before our nativity. But at this time when the circulation of the blood is no longer continued through the placenta, that suffocating sensation which we feel about the præcordia when we are in want of fresh air, disagreeably affects the infant and all the muscles of the body are excited into action to relieve this oppression; those of the breast, ribs and diaphragm are found to answer this purpose; and thus respiration is discovered; and it is continued throughout our lives as long as oppression begins to occur." Darwin is not daunted even by the clear indications of instinct presented by social insects, for he says, "If we were better acquainted with the histories of those insects which are formed into societies, as the bees, wasps and ants, I make no doubt but we should find that their arts and improvements are not so similar and uniform as they now appear to us, but that they arose in the same manner from experience and tradition, as the arts of our own species, though their reasoning is from fewer ideas, and is busied with fewer objects and is exerted with less energy." Similar views were developed by Condillac in his *Traité des Animaux* published in 1766.

What had come largely through the writings of Aquinas and his followers to be typical catholic doctrine concerning the mental life of animals found a very able defender in S. H. Reimarus, a prominent prelate of the church, but at the same time an industrious worker in the field of animal behavior. His chief work, *Allgemeine Betrachtungen über die Triebe der Thiere,* remained for a long time the most extensive and thorough treatise on the subject. It passed through four German editions and was translated into French and into Dutch, and soon came to be regarded as a standard authority. The views of LeRoy, Erasmus Darwin and Condillac are subjected to a rigorous criticism which in most respects must be regarded as very well founded. The labors of Reaumur, Rösel von Rösenhof, Huber, Bonnet, Buffon, Spallanzani and other naturalists of the seventeenth and early part of the eighteenth centuries had added greatly to our knowledge of the instinctive behavior of animals, and Reimarus, from his wide acquaintance with literature and from his own experience, had little difficulty in making out a strong case for instinct. The key-note of the work is expressed in the title of an earlier treatise *Instinctus brutorum existensis Dei, eiusdemque sapientissimi, indicem,* issued in 1725. The wonderful instincts of animals cannot be explained on the basis of acquired habits; they are innate endowments, perfectly adapted to secure the welfare of the individual animal or its progeny, and hence an irrefragable testimony to the wisdom and beneficence of the Creator. Reimarus was strongly influenced by Aristotle and St. Thomas Aquinas. He is at great pains to show that there is a fundamental difference between instinct and reason, and that man alone has true rationality. He concedes to the animals perceptions, memory, volition and the ability to learn; but he denies that they have abstract or general ideas or any power of passing from one representation to another. By numerous other writers animal instinct came to be dwelt upon as affording some of the most conclusive evidence of design. Paley dilates upon it at length in his *Natural Theology,* and one of the volumes of the Bridgewater treatises is devoted to this fruitful topic.

Throughout human history there have been several motives behind the various divergent opinions that have been held in regard to animal psychology. The impulse of the sympathetic lover of animals to attribute to his dumb friends and dependents a generous meed of intelligence has always been a more or less potent influence. And then there is the temptation to tell as remarkable a tale as possible of the performances of the creatures described. Both these tendencies frequently lead to reading into an animal's actions an unwarrantable amount of sagacity. But more powerful than these motives, especially during the Christian era, have been the various theological prepossessions of different schools. In the 17th and 18th centuries we meet with two opposed tendencies in the interpretation of animal behavior; one toward attributing the actions of animals to the same faculties that are possessed by human beings and leading to a limitation of the sphere of instinct, or even to denying instinct altogether; the other toward explaining animal behavior, so far as possible, in terms of instinct or automatism, with the limitation of reason and all higher mental attributes to man alone. The philosophical skeptics, in general, were partial toward the first; the defenders of the faith toward the second. The one class of writers attempted to link man and animal more closely together, and to show their fundamental kinship; the other tried to make the gap between man and animal as wide as possible, and to show that there is an essential difference between them. "After the error of atheism," says Descartes, "there is none which leads weak minds further from the path of virtue than the idea that the minds of animals resemble our own, and therefore that we have no greater right to a future life than have gnats and ants, while on the contrary, our mind is quite independent of the body, and does not necessarily perish with it."

The same considerations that inspired this utterance of Descartes still have weight in determining the attitude of modern students toward problems of animal behavior. In the conclusion of his interesting book on the *Psychology of Ants and of Higher Animals,* Father Wasmann, one of the foremost investigators of the behavior of social insects, writes in regard to modern evolutionary psychology that "By denying the existence of the essential difference between animal and human psychic faculties this psychology not only raises brutes to the dignity of man, but degrades man to the level of the brute. Would to God that this were done in theory only; but alas! the practical consequence of this false theory is the demoralization and brutalization of man."

There is no denying the serious import of the problems about which comparative psychologists do battle. But even if the victory should fall to the most materialistic of the contending parties it is hardly to be expected that the consequences would be as dire as Wasmann surmises. We are bid to beware of the same old scarecrow that has so often appeared in the path of scientific progress. But its aspect is growing less terrible as time passes, and it is always the part of the man of science to go straight ahead as if it were not in existence.

The first to grapple in a very serious way with the problem of the evolution of instinct was Lamarck, although we meet with suggestions in regard to the inheritance of the effects of habits in the writings of LeRoy. Lamarck regarded the evolution of animals as brought about, to a very large extent, by psychic factors. His three primary divisions of the animal kingdom, the apathetic, the sensitive and the intelligent animals, are based on psychological distinctions. The apathetic animals, such as the infusoria, polyps, etc., are, like plants, irritable, but devoid of consciousness and spontaneity. The transition from the apathetic to the sensitive animals comes with the development of a nervous system which was erroneously regarded as absent in some of the higher members of the apathetic group. Consciousness first appears in a vague form, but as organization advances and the nervous system and sense organs become more specialized and perfected, consciousness comes to assume more of a guiding rôle in the process of evolution. Everywhere consciousness is considered by Lamarck as dependent upon the organization of the nervous system, but as he is an "interactionist" he regards the activities of animals as initiated to a large extent by their feelings and desires.

As is well known, Lamarck explained instinct as inherited habit; but habits depend upon antecedent desires of the animal; these lead to efforts by which the desires may be satisfied, and by frequent repetition the acts thus prompted become habitual and are passed on as inherited proclivities to following generations.

With the appearance of wants determination of action becomes gradually transferred from the outside of the organism to the inside. New wants engender new habits and give rise to new organs. Instinct is regarded as internal impulsion instead of response to outer stimuli. It stands sharply marked off from the activities, however complex, of the lower organisms whose behavior is entirely determined by their environment.

With the advent of the vertebrates with their well-developed brain we have the appearance of intelligence and free will. Lamarck sedulously avoids the anthropomorphism of many previous writers in maintaining that intelligence and will can arise only in higher animals which have the requisite nervous organization. With the perfecting of this organization the higher mental faculties become further developed, and reach their culmination in the mind of man which is regarded as the outcome of a continuous process of evolution.

Although much had been written on the instincts and habits of animals in the half-century following Lamarck, there was but little contributed to the doctrine of mental evolution until we come to Herbert Spencer, who undoubtedly ranks as one of the greatest of all genetic psychologists. Spencer's *Principles of Psychology* was published in 1855, but several years later after the Darwinian theory had been promulgated it was reissued in a revised and considerably enlarged form. His treatment of life and mind from the common standpoint of the adjustment of internal relations to external relations, his derivation of instinct from reflex action, his filiation of the process of reasoning with perception, his attempt to show that no sharp distinction can be drawn between instinct and reason, his efforts to give an account of the origin of the intuitions of space and time and the fundamental forms of thinking in terms of experience gradually accumulated through inheritance, and his theories of the genesis of moral impulses and æsthetic sentiments, are among the many notable features of this very original and closely reasoned book.

Spencer was a believer in the transmission of acquired characters, and much of his psychological speculation is based upon this doctrine. Many of his cherished deductions, however ably wrought out, will have to be discarded if the effects of experience, as so many biologists now believe, are not transmitted to the following generation. But if the foundation of many of Spencer's doctrines were to be removed, much of permanent value would nevertheless remain unshaken. The genetic method in the study of psychology, as well as in many other fields of thought, owes much to Spencer's illuminating thought and stimulating influence.

Only four years elapsed between the publication of Spencer's *Psychology* and the appearance of Darwin's *Origin of Species*. The latter work marked an epoch in the history of psychology as well as of biology. Darwin's theory of natural selection afforded a means of explaining the evolution of instincts, as of corporeal structures, by the slow accumulation of favorable variations. In the chapter on "Instinct" in the *Origin of Species,* Darwin showed that even wonderful and complex instincts such as those of the hive bee did not present insuperable difficulties to his theory. Could the theory be extended to explain the derivation and evolution of intelligence and possibly also the development of the human mind itself from that of lower forms?

In the *Descent of Man* Darwin attempts to show that the mind of man is fundamentally the same in kind as that of the animals, and differs only in degree of development. He attempts to show that the moral sense which had been often held up as man's peculiar possession and glory is an outcome of the social instincts and emotions found in higher animals. Such conclusions, with their far-reaching consequences, naturally aroused strong opposition on the part of many conservative people, while at the same time they afforded an inspiring outlook to Darwin's followers. Attempts to trace the genesis of human faculties were the natural outcome of the stimulus which Darwin gave to the study of comparative psychology, just as attempts to trace the lines of descent of various groups of the animal kingdom followed closely upon the early battles over the mutability of species. Romanes' volumes on *Animal Intelligence, Mental Evolution in Animals* and

Mental Evolution in Man are among the best-known products of this movement.

There was a strong tendency toward anthropomorphism in many post-Darwinian writers, as there was in several of the skeptics of the eighteenth century. The effort to show that the human mind evolved from the animal mind led many to read an undue amount of intelligence into the activities of animals. The works of Perty, Büchner, Vogt, Brehm, and to a certain extent Romanes afford illustrations of this failing. What Wasmann calls "humanizing the brute" became a favorite theme. Several writers of the early post-Darwinian period restrained within reasonable limits whatever bias they may have had toward anthropomorphism, and contributed observations and experiments which have thrown much light on the problems of animal psychology. Among these may be mentioned Lubbock, Forel, Lloyd Morgan, Dr. and Mrs. Peckham, McCook and many others. The scholarly works of Groos on *The Play of Animals* and *The Play of Man* are excellent examples of the application of Darwinian principles to the interpretation of behavior.

Among post-Darwinian authors on animal psychology there soon arose a division between the neo-Darwinians who attributed evolution mainly or solely to natural selection, and the neo-Lamarckians who attached much greater importance to the inheritance of the effects of experience. This division was foreshadowed by the different degrees of importance attached by Darwin and Spencer to the factors of natural selection and the transmission of acquired characters. Darwin accepted the latter theory, but assigned to the Lamarckian factor a subordinate rôle as compared with natural selection. Spencer, who had already elaborated his system of psychology on the basis of the Lamarckian theory, naturally attached great weight to that doctrine, but when the theory of natural selection was announced he cordially received it, but he appealed to it mainly as a helpful subsidiary hypothesis.

Since Weismann made his attack upon the Lamarckian theory he has been followed by a considerable number of psychologists, such as Lloyd Morgan, Forel, Groos, Whitman, Baldwin and Zeigler, who reject entirely the doctrine that acquired characters are transmitted. Among the neo-Lamarckians who, though somewhat in the minority, still represent a flourishing school, there are all sorts of views regarding the potency of natural selection, some writers going so far as to cast the theory aside as a visionary and groundless speculation. Romanes, Eimer, Haeckel, Hering, Wundt, Cope, Semon and Pauly are among the principal writers of this school who have concerned themselves with comparative psychology. The combination of vitalism and Lamarckism which is presented in the writings of Pauly and Francé affords, in the opinion of its adherents, a method of accounting for the development of adaptations quite independently of natural selection. This is done by endowing the organism with a teleological principle which makes all the adjustments required to meet its needs; these adjustments are then transmitted to the descendants and thus gradually effect a progressive adaptive modification of the species.

Without raising the question as to whether the vitalistic explanation of adaptation really explains anything, it might be remarked that, since a teleologically working principle is assumed as the basis for the acquired adjustments of the individual, the same principle might also be evoked to guide the entire course of evolution without appealing to an agency of such questionable potency as the Lamarckian factor. *Entia non sunt multiplicanda praeter necessitatem.* If we invoke any vitalistic agencies or teleological principles we might as well give them plenty to do.

The theory of organic evolution having been firmly established, and the conviction having become quite general among psychologists that the human mind has resulted by a continuous process of development from the mind of animals, the controversial interest in various questions that stimulated the earlier post-Darwinian students of the animal mind has to a considerable extent subsided. The effort to trace the evolution of particular instincts and mental faculties continues to afford an absorbing and fruitful occupation, but such work is pursued, not so much with the aim of establishing the fact of evolution in a particular field, as of illuminating the subject in the light of its historical development. In human psychology the genetic method of study is pursued to a large extent in the works of Stanley Hall, Groos and Baldwin, and in the recent volumes of Kirkpatrick on *Genetic Psychology* and of Parmelee on *Human Behavior*. Modern "philosophy of education" has been influenced in no small degree by studies and speculations in comparative psychology, and especially in this country by those of Stanley Hall and his school. The doctrine of recapitulation figures quite largely in the writings of this school, and, while the results of its application have not always been happy, the general influence of Hall and his followers has given a strong stimulus to genetic psychology and the scientific study of problems of education.

Much attention has been devoted to the experimental analysis of instinct. The complex instincts of crustaceans and insects have been shown by means of operative experiments on the nervous system to be, to a large extent at least, capable of analysis into reflex activities of the various segments. A brainless crayfish will walk, eat food, reject innutritious substances, defend itself when seized, and perform various other complex activities. When any of the segmental ganglia of the nervous cord are cut off from communication with the others by severing the connectives, the appendages of the corresponding segment will respond adaptively to many stimuli that are applied to them. Many of the more complex activities of the animal may be explained as chain reflexes in which one act affords the stimulus to the performance of other acts. The behavior of the whole animal might be regarded as the result of a sort of social cooperation of the activities of its various quasi-independent nervous ganglia. One cannot say that the seat of instinct in such an animal is in the brain or any other part of the nervous system. The instincts of the animal are the outcome of its general organization; they are the expression of the workings of the organic mechanism. Experiments indicate that the same conclusion applies to the instinctive behavior of vertebrates. Whether or not we regard instinct with Herbert Spencer, as "compound reflex action," we may be justified in concluding that it is everywhere a function of organization.

With the same aim at analysis a large amount of work in recent years has been devoted to the subject of tropisms. Loeb's celebrated theory of orientation attempts to explain these directed movements of animals in terms of reflex action; many instincts of animals are apparently the outcome of these tropic reactions; even in the higher animals it is probable that certain tropic responses are still retained. As the tropisms are discussed more fully in a later chapter this brief indication of their importance in the development of animal psychology may perhaps suffice.

From the standpoint of analysis as well as that of evolution, a considerable interest attaches to the behavior of the simplest forms of life. Here, if anywhere, one might expect behavior to be capable of analysis into physical and chemical processes. The behavior of the Protozoa for this reason has attracted a number of careful workers who have endeavored to test how far such behavior can be explained in terms of simpler factors. Jennings in particular has done a large amount of careful observational work in this field; he has shown in the case of Amœba, which is often referred to as an almost structureless mass of jelly, that the behavior is surprisingly complex, and at present incapable of being explained in terms of physical and chemical laws. This does not imply that the behavior of Amœba is, in the last analysis, incapable of such explanation; it simply means that our present knowledge is inadequate for this task. Even the simplest organism is a very complex structure from the standpoint of the chemist. And it is not to be wondered at that the simplest creatures often act in ways which we can neither predict nor explain. Minute study of the behavior of the lowest organisms, however, has revealed a remarkable amount of uniformity. The activities of these forms are stereotyped, yet plastic, and while no intelligence has been proven to occur in any of them, their behavior is often capable of modifications in various ways in adaptation to changed conditions of life.

The behavior not only of the Protozoa but of all higher classes of animals has been studied in the last few years with a great increase of zeal and thoroughness. The activities of hydroids, jelly-fish, worms, mollusks, echinoderms, crustaceans, as well as insects, and vertebrates, have engaged the attention of a small army of investigators who are rapidly amassing a vast store of detailed knowledge. A very few years ago there was established a special periodical, *The Journal of Animal Behavior,* devoted exclusively to papers on animal psychology, while an increasing amount of literature on the subject is going into other channels.

The days of anecdotal psychology, when it was the fashion to bring together stories from various sources illustrative of animal sagacity, are passing. The psychological interpretation of animal behavior is a subject that abounds in pitfalls for the unwary. To find out what probably goes on in an animal's mind requires close and continuous observation, and usually experiments under carefully controlled conditions. The careful experimental work of Thorndike, Cole, Yerkes, Hobhouse, Small and many other investigators, has given us a more exact knowledge of the mental activities of the animals studied than would have been possible through the collection of any quantity of scattered observations. The results have sometimes proven disappointing to zealous champions of the high mental development of their animal friends.

There is little ground for believing that animals have abstract or general ideas, or the power of deliberate reasoning, but there is considerable experimental evidence that they have ideas of a simple sort and a certain power of inference. Careful investigators at present show a wholesome caution about ascribing to the mind of the animal more than the facts really justify. Lloyd Morgan has laid down the principle, since known as the principle of Morgan, that no act should be ascribed to a higher mental faculty if it can be satisfactorily accounted for in terms of a lower one. The burden of proof is thus placed upon those who contend for the superior endowments of the animal mind. What we want are not stories of performances which might have involved unusual intelligence, but records of achievements which cannot be accomplished except by means of unusual intelligence. In the latter case only are we justified in ascribing to the animal the mental attribute in question. In following the principle of Morgan we may often fail to give to the animal full credit for the faculties it may really possess, but our conclusions will be sound so far as they go.

II

THE EVOLUTION OF PARENTAL CARE

INSTINCTS for the care of young extend far down in the animal kingdom and their origin therefore dates back to an early period in the history of the earth. The important rôle which these instincts have played in the evolution of animal life,—a rôle which has increased in importance as animals have become more highly evolved,—renders the subject of their origin and course of evolution one of especial interest to the comparative psychologist. With a full realization of the fact that phylogeny is a treacherous field I have nevertheless ventured in the following account to outline the probable way in which animals came to care for their offspring, and to point out briefly how parental care has been instrumental in shaping the more advanced stages of the evolutionary process.

In several respects, notably in relation to social and ethical evolution, the institution of parental care has formed the foundation for higher stages of development. Organized societies in animals generally have their beginning in the expansion of the family. In some insects, for instance, such as the ants, bees, and social wasps, various gradations may be traced between the simple family and the highly organized social state. Many insect communities consist merely of an enormous family resulting from a single female parent; and when the community includes more than this the condition is generally a secondary outgrowth of the domestic group.

In the care of parents for their young we probably find also the first traces of altruistic instinct. Family life is impossible on the basis of purely egoistic behavior. Some altruism, however weak and limited in its scope, is the essential condition of the family group. In low forms it is limited to the care for offspring; later it may include other members of the species beyond the limits of the family; but it is a long time before it extends its blessings at all widely. Most creatures care not a fig for the welfare of any but their own immediate kin; and where we find any consideration bestowed upon alien forms, as in the fostering of aphids by ants, it is done for the sake of something to be gained in return. Animals in general live under conditions in which they cannot afford disinterested benevolence. While the long hard struggle for existence may have bred tender feelings and unselfish impulses it has produced them for the same ultimate purpose that is subserved by sharp claws and good teeth,—the survival and perpetuation of the species. Parental care is one of Nature's devices for race survival. But very few of the devices which Nature has hit upon have influenced so profoundly the course of evolution in the higher animals.

We cannot of course follow step by step all the stages in the evolution of the parental instincts and feelings, but by a comparative survey of the animal kingdom it is possible to construct, with some degree of probability, the main outlines of this development. Among the lower invertebrates the offspring have to shift for themselves at their very first appearance upon the stage of life. There are sometimes devices such as brood pouches for the protection of the eggs or young, but any active solicitude of parents for their offspring does not appear until we reach the higher invertebrate animals. This lack of parental interest is well illustrated by the behavior of an amphipod crustacean, Amphithoe, which the writer studied in some detail a few years ago. In this form the eggs, and also the young for a few days after being hatched, are carried in a brood pouch on the under side of the body. When sufficiently agile the young make their way out of the brood pouch and swim away, the mother paying no more attention to them than to any other animate object. Indeed the carnivorous habits of this species make it more or less dangerous for the young to tarry long in the vicinity of their parent. Several times I have caught the young in a fine pair of forceps and offered them to the mother, who ate them without the least compunction. It is only in a grossly material sense, therefore, that Amphithoe can be said to be fond of its offspring.

So far as the writer is aware the same utter lack of maternal sentiment characterizes all the crustaceans as well as the numerous varieties of worms and mollusks. Among the arachnids Fabre has described how the female scorpion assists her young to hatch by carefully tearing away the egg membranes with her jaws. When the tiny scorpions are liberated they have the curious habit of mounting upon the back of the mother, who for a period of several days remains closely confined to her nest. In the spiders, although as a rule only an attitude of hostility is manifested toward other members of their own kind, the running spider Lycosa carries her cocoon about with her and when the young spiderlings are hatched they cling in a squirming mass to her body. The mother does not feed or actively care for her young in any way, and it is doubtful if maternal care goes further than a sort of good-natured tolerance of her living burden.

There is much evidence for the supposition that the first step in the evolution of parental care was taken in the formation of instincts to secure the proper environment for the development of the eggs. Instincts for depositing eggs in places which afford food for the young, instincts for making cocoons or other receptacles for the eggs, and instincts for concealing the eggs from the attacks of other animals are common in animals which are too primitive to exhibit any care for, or even recognition of their own offspring. Many mollusks plaster their eggs on stones or aquatic plants or bury them in gelatinous masses in the sand, but they certainly have not the least glimmer of an idea concerning the free swimming larvæ to which the eggs will give rise. The cabbage butterfly instinctively deposits its eggs on cabbages or other cruciferous plants, the bot fly oviposits upon the hairs of horses and cattle, and the May fly drops its eggs into a pond or stream, but it is utterly out of the question to suppose that any of these creatures has the remotest notion of the larvæ that will issue from its eggs, much less of the relation of the environment of the eggs to the needs of larval life.

A further step in the direction of parental care is taken by the solitary wasps. In many species the female digs a hole and then goes in search of a particular kind of insect or spider to serve as food for her young grub. The victim is stung in such a way that it is paralyzed but not killed, so that the young can live upon food that is not decayed. Then the prey is stored in the hole, an egg laid upon it, and the hole filled up with dirt and left, the mother never coming back to see how things fare with her young, nor concerning herself further with its welfare. In fact, most of these wasps never see their own progeny, and show no signs of recognition when the larvæ are shown to them. All the wonderful instinctive acts by which the solitary wasps provide so well for the needs of their larvæ are blindly performed, and give no indication of any feeling of parental affection, even of the most rudimentary sort.

A more advanced stage in the evolution of parental care comes with the appearance of instincts for more or less continuous care of the eggs after they are laid. If the cocoon of the running spider is taken away from her, which is done only after a certain resistance, she will eagerly seize it again if she happens to encounter it. The egg mass is treated as an object of interest, although the young which issue from it are regarded with indifference. Instincts for remaining with the eggs for a longer or shorter time after they are deposited are not infrequent among fishes, and especially among those species which expend some labor in the construction of a nest. Generally this task is performed by the male, as in the sticklebacks and the common Amia or dogfish of our ponds and streams. The males of these fishes remain in or near the nest after the eggs are laid, and they keep on the alert to drive away any intruder that ventures too near.

The Amphibia, which as a group are remarkable for queer breeding habits, show in many cases primitive instincts for guarding or at least remaining close by the eggs during the early stages of their development, although most species, as in our ordinary frogs and toads, simply abandon their eggs as soon as they are deposited. The newt Desmognathus lays its eggs in a small hollow and remains near them for some time. The snake-like cæcilians coil about their egg masses, and certain species of frogs carry eggs in pouches on the back or in sacs connected with the throat. One of the most peculiar cases is afforded by the obstetrical toad of Europe in which the male carries the string of eggs coiled about his hind legs until the young are ready to hatch.

While the Amphibia in some cases exhibit a certain care for their eggs, they all appear to be utterly indifferent to their young. One reason for this is the fact that the young usually live in the water while the parents are often terrestrial, but another reason is doubtless to be found in the low psychic development of these animals.

Reptiles as a class concern themselves very little about their progeny. The latter are quite well able to take care of themselves upon their first introduction into the world. Alligators are said to watch over the places where their eggs are buried in the sand, and pythons coil around their eggs and help to incubate them by the warmth afforded by their bodies. Solicitude for their eggs is, however, very rare among the reptiles, and active care for their young is practically absent.

With the birds, which as a group are remarkable for their parental and fostering instincts, care for the eggs appears to be universal, and with rare exceptions the birds sit upon the eggs until they are hatched. There has been much speculation concerning the origin of this curious instinct of incubation. As Whitman has remarked, "the incubation instinct was supposed to have arisen *after* the birds had arrived and laid their eggs, which would have been left to rot had not some birds just blundered into cuddling over them and rescued the line from extinction." A little reflection makes it evident that such an origin is clearly impossible, and that we must go back probably to the cold-blooded reptilian ancestors of the birds for the beginnings of the instinct. A comparative survey of the behavior of the more primitive animals toward their eggs makes it probable that the instinct of incubation grew out of the instinct to remain in or near the place where the eggs are deposited for the purpose of protecting them. Lying near or brooding over the eggs may have afforded, even in the cold-blooded ancestors of the birds, sufficient heat to make the eggs develop with increased rapidity. The advantage thus accruing to the species may have caused the protecting instinct to develop further into a true instinct for incubation. With the development of warm bloodedness which went on during the evolution of the birds from the reptiles the supplying of artificial heat, at first only a means of hastening development, became an indispensable condition of development. Dependence upon artificial heat must have been evolved *pari passu* with the development of the instinct for incubation. Certainly the latter never could have been developed after the former had been established.

There is much evidence to show that the next step toward the development of parental affection was brought about by the extension of care for eggs to what comes out of the eggs. Little more than a feeble beginning of such an extension occurs among some of the arachnids to which we have already alluded. In most insects, although provision for the eggs is common, the parents, with rare exceptions, are utterly indifferent to their young. Among the social insects, however, such as the ants and bees, the young grubs are tended with scrupulous care. In the solitary bees and in many of the more primitive social species the eggs are laid with sufficient provisions for the entire life of the larvæ and then left without further attention. The transition from this condition to one in which food is brought to the cells after the larvæ are hatched is an easy and natural development. And as we pass to the more highly developed social groups such as the hive bees the instincts for taking care of the larvæ become more specialized and more complex.

Among the various species of fishes that bestow some care upon their eggs there are some forms that pay no particular attention to their newly hatched young which scatter as soon as they emerge from the coverings of the eggs. In other cases such as the dogfish Amia the protecting instinct is extended to the young brood. The male parent swims about with his school of small fry and keeps many enemies at a safe distance, for he is an alert and valiant defender of his own. In the course of a few weeks, however, the family ties are broken, the little fishes become dispersed far and wide, and parental solicitude, having subserved its purpose of affording protection when it was most needed, is manifested no more.

When care becomes extended from the eggs to the young a course of development is begun in which relatively more and more care is bestowed upon the offspring as we pass to higher forms. Instead of a large number of progeny left to shift for themselves with a consequent great loss of life, we find in the higher animals a decrease in the number of offspring combined with an increase in the care and attention devoted to each. The young become at the same time less able to take care of themselves and are dependent upon their parents for longer periods. And along with these changes there is an increase of sympathy, affection and the various emotions that come into play in the family relation.

This is well shown among the birds. The lower birds lay many eggs either in crude nests or none. The young birds which are quite active when hatched do not remain long under their parents' care, and many are lost. The higher song birds, on the other hand, lay few eggs in a well-prepared nest, and the young which remain in a weak and helpless state for a considerable time after hatching are fed by their parents, kept clean, and protected from various enemies. There are few more fascinating pictures of domestic life than those afforded by the little family group in many of the higher birds.

Among the mammals we may trace a similar line of evolution. The suckling of young presupposes a certain tolerance, if not regard, on the part of the mother for her offspring. Had there not been among the ancestors of the mammals a fairly close association between the parents and their offspring during the infancy of the latter there obviously could not have been evolved the mammary glands and other adaptations for suckling the young which are among the most fundamental and distinctive features of mammalian structure. Instinct and organization are everywhere closely correlated and act and react upon one another during the course of evolution. The mammals afford an interesting instance of the way in which instincts of parental care have been instrumental in developing certain fundamental peculiarities of bodily organization.

Certain writers of the associationist school of psychology have endeavored to explain why animals regard their young with affection on the basis of the relief the mother experiences in having the milk removed from her mammary glands. Bain would have us believe that maternal love was compounded out of numerous agreeable sensations of touch experienced in handling the soft bodies of infants. Why the mothers do not develop an equal fondness for velvet-covered cushions the theory does not make clear. Such explanations appear eminently absurd in the light of a comparative study of the relations of parents to offspring in various groups of animals. Parental care must have antedated the giving of milk, and it is probable that without parental affection there would be little more contact between parent and offspring than there is among fishes and amphibians. From the genetic standpoint both explanations put the cart before the horse.

Among animals generally parental affection is rather strictly limited to the period of infancy, after which there is a disregard or indifference that contrasts strangely with our own natural sentiments. The affections of animals, like most of their other characteristics, are quite closely subordinated to the needs of the species; when the young are able to make their way in the world alone the function of parental love is past, and the feeling rapidly becomes extinct.

As we approach man we find a lengthening of the period of infancy and a prolongation of the time during which the parents bestow their care and affection upon their offspring. As John Fiske has shown, the lengthening of infancy affords opportunity for the young to acquire experience and perfect themselves in the varied activities which are demanded in the life of a highly evolved animal. Where, as in higher forms, success in life depends relatively more on intelligence than blind instinct it is important that there should be a period of education in which the young animal is more or less shielded from the hardships and dangers with which it will have to cope in later life. Our simian cousins remain with their young for a long period, and exhibit a degree of tenderness for them that is little short of that shown by human beings. In the *Descent of Man,* Darwin relates that "Rengger observed an American monkey (a Cebus) carefully driving the flies which plagued her infant; and Duvancel saw a Hylobates washing the faces of her young ones in a stream. So intense is the grief of female monkeys for the loss of their young, that it invariably caused the death of certain kinds kept under confinement by Brehm in North Africa. Orphan monkeys were always adopted and carefully guarded by other monkeys, both male and female."

It is a far cry from the egg-protecting instincts of primitive animals to the love of a human mother for her children. But the animal kingdom presents us with many of the intervening stages of evolution. The most primitive instinct and the most developed affection work toward the same end,—the perpetuation of the race. Both are parts of the life process which is everywhere occupied with the business of its own maintenance.

The two phases of this process represented by self-preservation and race preservation have become elaborated *pari passu* in the course of evolution. If our preceding account is correct, parental care and all the social and ethical instincts to which it forms the preparatory stage of development may be regarded as an outgrowth of the process of reproduction. To the simple acts of egg laying there came to be added other activities which make for the welfare of the progeny, leading on to active solicitude for the young, and thence to social instincts which finally blossom out into the rich endowment of altruistic emotions and sentiments of highly evolved social life. It is in reproduction, which is essentially an altruistic activity, that we must seek for the roots of altruism. Egoism and altruism in their primal manifestations are coeval rather than successive phenomena. The primitive organism which grows and divides by fission shows us the germ of both of these traits.

REFERENCES

BAIN, A. The emotions and the will. 4th ed., 1899.

DARWIN, C. The descent of man. N. Y., 1874.

FABRE, J. H. Souvenirs entomologiques, T. 9.

FISKE, J. The meaning of infancy. N. Y., 1909.

HOLMES, S. J. Observations on the habits and natural history of Amphithoe longimana. Biol. Bull. 2, 165, 1900.

MITCHELL, P. C. The childhood of animals. London, 1912.

MORGAN, C. L. Animal behavior. London, 1900.

PECKHAM, G. W. and E. G. On the instincts and habits of the solitary wasps. Bull. No. 2, Wis. Geol. Nat. Hist. Soc., 1898.

PYCRAFT, W. P. Infancy of animals. N. Y., 1913.

Reighard, J. The natural history of Amia calva Linnæus. Mark Anniversary Vol. p. 57, 1903.

Romanes, G. J. Animal intelligence. N. Y., 1883.

Sutherland, A. Origin and development of the moral instinct. London, 1898.

Whitman, C. O. Animal behavior. Biol. Lectures, Marine Biol. Lab. Woods Hole, 1898.

III

THE TROPISMS AND THEIR RELATION TO MORE COMPLEX MODES OF BEHAVIOR

THE subject of animal behavior has been of interest to human beings from the earliest times, but it has not been taken very seriously until a comparatively recent date. The ways of animals were considered curious, interesting and in many ways useful things to know about, but the great theoretical import of animal psychology was unsuspected until it came to be recognized that our own minds are the outgrowth of the animal mind, and that to obtain a truly scientific human psychology it is necessary to have a clear insight into the psychology of the lower animals from which we are descended. Near the middle of the nineteenth century Herbert Spencer enunciated the principle that, "If the doctrine of evolution be true the inevitable implication is that mind can be understood only by observing how mind is evolved," and he boldly plunged forward upon an undertaking to remodel the science of psychology from the genetic standpoint. The result was the publication in 1855, four years before the appearance of the *Origin of Species,* of the *Principles of Psychology,* a work which for sheer originality, independence of treatment and profound grasp of the subject stands almost without a rival in the history of the science.

Notwithstanding the work of Spencer, genetic psychology was given perhaps its greatest impetus by Darwin, not only through his influence in establishing the general doctrine of organic evolution, but also through his careful work on, and illuminating treatment of the mental life of animals. The admirable and original chapter on Instinct in the *Origin of Species,* the chapters on the comparison of the mental powers of man and the lower animals in the *Descent of Man,* and the work on *The Expression of the Emotions in Man and Animals,* were all substantial contributions to the science, which were very influential in stimulating further work.

It is not my intention to treat of studies of animal behavior undertaken from the standpoint of evolution, but to discuss another and in many respects complementary aspect of the subject, that of analysis, or the effort to discover the causal mechanism of animal activities by resolving them into their component factors. The analytical study of behavior is simply a consequence of extending to animal psychology the methods of experimental investigation so largely employed in the physical sciences and which are coming more and more to be employed in biology and in the laboratory investigations of the psychology of man. The results thus far won may be meagre, but judging from the increasing number of trained investigators who are devoting themselves to the work, we may look forward to a rapid increase in our knowledge and insight.

From the standpoint of analysis the subject of tropisms is one of great import. Certain stimuli exercise a directive effect upon the movements of animals, causing them to go toward or away from the source of stimulation. The moth flies toward a candle; infusorians gather in regions of dilute acids and avoid regions of too great heat or cold; certain caterpillars tend to crawl opposite the direction of the force of gravity. These directed movements are commonly called tropisms but there is a variety of opinions regarding the kinds of behavior to which the term tropism may be applied and usage has not settled authoritatively upon any rigid definition of the word. We shall therefore use the word in a somewhat broad and indefinite sense.

Tropisms have long been recognized in plants. The familiar phenomenon of the turning of plants to the sun was termed heliotropism by De Candolle in 1835, and he, in common with several other botanists in the early and middle parts of the nineteenth century, regarded this turning as a direct and more or less mechanical effect of sunlight upon the tissues of the plant. Sachs on the other hand emphasized the aspect of irritability in tropisms, and maintained that it is the direction in which the rays of light penetrate the tissues of the plant and not merely the different degrees of illumination on the two sides, that determines the direction of turning. The work of Sachs on plants directed the attention of Loeb to the phenomena of tropisms in animals, and also furnished him with some of the fundamental conceptions of his own celebrated theory. Loeb's first paper on tropisms of any considerable length was entitled *The Heliotropism of Animals and its Agreement with the Heliotropism of Plants.* The publication of this paper marked an epoch in the analytical study of animal behavior. Previous to this time the tropic responses of animals were interpreted as the expression of the predilections or conscious choice of animals for certain kinds of stimulation. Graber, Sir John Lubbock and Paul Bert had studied the effect of colored lights upon animals and discovered that certain species congregated most abundantly under light of a certain color, while other species would gather in greater numbers under light of a different color. These aggregations were therefore considered as an index of the kind of color most pleasing to the æsthetic or other sensibilities of the animals. Movements toward or away from lights were accounted for in a similar way. Earwigs and cockroaches were supposed to crawl away in secluded places because they like the dark and butterflies were supposed to congregate in sunny spots because they enjoy the sensation afforded by the sunshine. A somewhat more anthropomorphic interpretation of a tropism was suggested by Romanes in discussing why the moth flies into the flame of a candle. The conclusion arrived at was that the moth was drawn to the fatal flame out of curiosity, or the desire of investigating what manner of strange object a candle flame might be.

The theory developed in Loeb's *Heliotropism* stands in a sharp contrast to the anthropomorphic views of his predecessors. Orientation of animals to light is supposed to take place in a more or less mechanical fashion like the orientation of plants. "These tropisms," he says, "are identical for animals and plants. The explanation of them depends first upon the specific irritability of certain elements of the body surface, and second, upon the relations of symmetry of the body. Symmetrical elements at the surface of the body have the same irritability; unsymmetrical elements have a different irritability. Those nearer the oral pole possess an irritability greater than that of those near the aboral pole. These circumstances force an animal to orient itself toward a source of stimulation in such a way that symmetrical points on the surface of the body are stimulated equally. In this way the animals are led without will of their own either toward the source of the stimulus or away from it." The moth flies into the flame, not out of curiosity or any other conscious motive, but simply because it cannot help it.

In a very instructive series of experiments Loeb showed that heliotropism in animals obeys the same laws as heliotropism in plants. In both plants and animals it is the direction of the rays that controls the direction of movement. In both plants and animals it is the rays nearer the violet spectrum that are the more potent in evoking the heliotropic response. In both plants and animals temperature, previous exposure to light and other external factors influence reactions to light in much the same way. Back of all the differences of form and function of plants and animals, and notwithstanding the higher organization of the animal world with its specialized sense organs and complex nervous systems, the living substance of organisms possesses certain fundamental common properties of irritability upon which the common and fundamental features of behavior which we call tropisms depend.

The theory of Loeb would sweep away all higher psychic factors in the realm of tropisms, and reduce the phenomena to comparatively simple manifestations of reflex irritability. Further he would explain much of the so-called instincts of animals as a result of these tropisms. Since the prospect of finding a mechanical or causal explanation of any feature of behavior is always an alluring one, it will be of interest to pass in review some of these cases of tropisms with the end of determining how far the reflex theory will carry us. And then we shall consider the relation of these tropisms to more complex forms of behavior.

An excellent illustration of a tropism is afforded by the light reactions of the larvæ of the marine worm *Arenicola*. These larvæ are oblong in shape, with two eye spots at the anterior end. Near either extremity there is a band of cilia by means of which the larvæ swim through the water. The larvæ are positive in their reactions to light, and will follow a light around in various directions. Orientation to light is brought about by bending the body to the stimulated side. If the larva is between two sources of light from which the rays intercept one another as they fall on the animal at an angle of ninety degrees, the larva will take a course midway between the two lights. If one light is turned off the larva bends immediately to the other one. By arranging a mirror so as to throw a small spot of light on different parts of the body, Mast has shown that when light is thrown into one eye there is a strong bend of the body toward the stimulated side. The parts behind the eye spot show no definite reaction. It is evident that orientation in this form is due to different intensities of illumination on two sides of the body. So far as can be ascertained orientation takes place directly and automatically, without any conscious decision on the part of the animal. The movements of the larva appear little more voluntary than the precise movements of certain Protozoa or the swarm spores of algæ. Let us pass to animals somewhat higher in the scale of life.

Some years ago when on the Atlantic coast at Woods Hole, Mass., I studied the behavior of various amphipod crustacea of that region and particularly the reactions of the terrestrial species commonly called sand fleas. It is a somewhat curious circumstance that the aquatic amphipods are negative to light and tend to keep in the darkest part of their environment while the terrestrial ones are usually positive. Positive phototaxis is the most pronounced in the most terrestrial of the species, the large *Talorchestia longicornis,* which lives in holes in the sand high up on the beach. When dug out of the sand these crustaceans usually lie curled up in a death feint, but when they become active they manifest a very strong tendency to hop toward the light. When brought into a room they may keep hopping toward a window with intervals of rest during the entire day. If they are placed in a dish one-half of which is shaded while the other half is exposed to the direct sunlight they will keep hopping toward the light until they are overcome by the heat of the sun's rays.

The smaller *Orchestia agilis,* which lives nearer the water's edge and frequently manifests a negative reaction to light, shows the same fatal degree of positive phototaxis when exposed for some time to strong sunlight. Does light orient these forms automatically and involuntarily as is apparently the case with the larvæ of *Arenicola?* There are several facts which favor such an interpretation. The persistent and apparently unreasonable nature of the response, its sudden reversal by certain external agents, and especially the fact that the witless creatures continue to go toward the light even when they are brought thereby into a region where the heat proves fatal to them, seem to bear out the conclusion that the phototaxis of these animals is in the nature of an involuntary or "forced" response. This view is strengthened by the results of certain experiments on individuals which were blinded on one side. These experiments were undertaken with the view of ascertaining something of the mechanism of orientation. The amphipods do not become oriented by bending the body toward the light, but by the unequal activity of the appendages on the two sides of the body. In forms with positive phototaxis it was found that blackening over one eye caused the amphipod to perform circus movements toward the normal side. In negatively phototactic species it was found that the same treatment caused circus movements in the reverse direction. It is probable therefore that impulses received by the eyes cross in the central nervous system and become carried to the appendages on the opposite side of the body, causing them to act with greater vigor, thus bringing the animal into a position of orientation. This supposition led to the experiment of cutting the brain lengthwise through the center in several species of arthropods and it was found that, although sensitiveness to light could be shown to remain, all power of orientation to light was entirely destroyed.

It will be of interest in this connection to consider the light reactions of a somewhat more highly organized arthropod, the water scorpion Ranatra. This insect lives near the banks of ponds and streams with the tip of its long breathing tube at the surface of the water and its raptorial fore legs held in a position for rapidly seizing any small passing creature which may be utilized for food. When Ranatra is taken out of the water it generally feigns death, assuming a perfectly rigid attitude which it retains through all sorts of maltreatment, even suffering its legs to be cut off or its body to be cut in pieces without betraying any signs of animation. By moving a light over the motionless insect it may gradually be brought out of its feint. The first noticeable signs of awakening are very slight movements of the head in response to the movements of the light. When the light is passed to one side of the body the head is rolled over ever so little toward that side. Move the light to the other side and the head tilts over slightly in that direction. Place the light in front of the body and the head bows down in front. Now carry the light behind the insect and the front of the head points slightly upward. These movements occur with perfect regularity in response to the movements of the light, and gradually increase in vigor and extent. After following the movements of the light with these definite movements of the head the insect slowly and awkwardly raises itself up and begins to follow the light with equally definite swaying movements of the body. If the light is to one side the legs on that side are flexed and the opposite legs extended. Passing the light over the body causes the reverse attitude. Hold the light in front of the body and the insect bows down in front in an attitude of abject submission. Carry the light behind the insect and it elevates the anterior part of its body and holds its head high in the air. These bodily attitudes are assumed with almost machine-like regularity. For each position of the light there is a corresponding position of the head and body.

After a little Ranatra will follow the movements of the light by walking slowly and awkwardly toward it, gradually increasing the vigor and rapidity of its response until it will rush toward the light with frenzied haste. It becomes oblivious to all else but the light, which seems to dominate its behavior entirely. If the source of light gives off a good deal of heat the insect will continue to go toward it until overcome by the heat. I have seen Ranatras when nearly killed by the heat of the lamp toward which they were attracted, slowly drawing themselves with the last remnants of their strength a little nearer to the fatal source of light.

Nothing could seem more mechanical or more obviously the result of domination by outer agencies than the phototaxis of this form. There are, however, some curious features of the behavior of Ranatra which are disclosed by other experiments and which indicate that this insect is something more than a mere "reflex machine." If one eye is blackened over there is a strong tendency for the insect to perform circus movements toward the normal side. Frequently as the insect veers over toward the normal side in going toward the light and thus brings the unblackened eye more and more out of the region of direct stimulation, a point is reached where there is hesitation, moving this way and that, accompanied by increasing uneasiness and excitement as if the creature were exasperated over its predicament. Sometimes the insect may get out of this situation by going completely around in a circle toward the normal side, or it may make a direct turn toward the blackened side and go toward the light. In several cases among Ranatras and Notonectas individuals which at first performed circus movements and succeeded in going to the light by a very irregular route finally came, after a number of trials, to go to the light in a nearly straight line. Other individuals went to the light in a nearly straight line from the first. In some cases covering all of one eye and all but the posterior face of the other did not prevent the insect from going in a nearly straight path toward the light. Other specimens would do the same with only a small part of the lateral face of one eye uncovered. In the latter case neither the lightest nor the darkest part of the visual field was kept before the eye. The insect behaved as if it were not guided by a mere reflex response, but had an awareness of the general space relations of its region, the relative position of the light and itself and of the movements necessary to bring itself toward the light. If such a general topographical sense seems too high a psychical endowment to be credited to so simple a creature, it must be remembered that other insects, notably the bees and wasps, have a much more definite and detailed cognizance of the topographical relations of their environment than anything in the behavior of Ranatra would call for. Simple and mechanical as much in the light reactions of Ranatra seems to be, there are many features of its phototaxis which are very difficult to explain on the basis of simple reflex orientation.

We might expect *a priori* to find that somewhere in the course of evolution the tropisms become more or less subordinated to higher forms of behavior. It is quite evident that much in the behavior of animals may be explained as a more or less simple manifestation of phototaxis, geotaxis, chemotaxis, and so on. The daily depth migrations of pelagic animals is traceable, to a considerable degree, to variations in the sense of the response to light and gravity. One circumstance that leads copepods to swim to the surface at night and go down in the daytime is because they are positive to weak light and negative to strong light. The negative reaction of centipedes, termites and many other organisms keeps them in dark and secluded situations.

The positive reactions of many worms and crustaceans to contact stimuli keep them in protected situations in various nooks and niches where they escape many of their enemies. The positive chemotaxis of many animals leads them into situations where they may find their food.

But one of the chief considerations which makes the study of tropisms of such importance is the fact that the tropisms enter as components into more complex activities of higher organisms. Tropisms in their purity are met with only in the simpler animals. As we pass up the scale of life these primary tendencies to action become broken up and combined with other forms of behavior, so that they are lost sight of in the more complex activities into which they enter as component factors.

A most interesting field of investigation in this connection is presented in the relation of phototaxis and vision. It is a field scarcely touched upon as only one investigator, Radl, has entered upon it with any seriousness. There seems to be a close connection in many animals, and especially in insects, between phototaxis and what are called compensatory movements. Place a lady-beetle on a turntable which is slowly rotated. The beetle begins to move its head and then its body opposite the direction of movement. Robber flies show the reaction especially well. The reaction depends upon the eyes because it no longer occurs when the eyes are blackened over. It does not depend upon the rotation of the insect's body. If the insect is placed in a cylinder on a stationary center and the cylinder rotated, the insect tends to walk around in the direction of rotation. A frog under the same circumstances will do the same thing. In these cases the animal reacts so as to keep, so far as possible, *in statu quo* with the visual field.

A beautiful illustration of this is afforded by the so-called rheotropism of fishes. Many fishes have the instinct to head up stream against the current. This trait has been shown by Lyon to be dependent upon a visual reflex. He placed fish in an aquarium with the lower side made of glass below which could be drawn a long piece of cloth with alternate black and white stripes on it, giving the appearance of a moving bottom. As the strip was pulled along the fish swam in the direction of movement. Reversing the motion caused the fish to turn about and swim to the other end of the aquarium. In another experiment fishes were placed in a long bottle. When this floated down stream the fishes all swam to the up stream end. When it was pulled up stream the fishes all swam to the opposite end. Fishes in a stream, passively carried along, have no means of becoming aware of their movements except by means of objects in their field of vision any more than a man in a balloon who is carried along in a current of air. This automatic tendency to keep in constant relations with the objects in their field of vision keeps them from being passively carried down stream. Many insects show the same trait in their flying against a breeze. Perhaps the instinct of hovering shown by many kinds of flies is an expression of the same fundamental tendency.

The automatic tendency to keep the body in a certain orientation to its field of vision which we find among crustaceans, insects and lower vertebrates, is to a greater or less extent replaced in forms with freely movable eyes by ocular movements which enable the moving animal to retain the same field of vision. Stalk-eyed crustaceans show compensatory movements of the eye stalks. Similar eye movements occur in fishes, amphibians and birds. A man at night more or less involuntarily directs his steps toward a single light in his horizon much as birds are drawn toward a lighthouse. Such orientation may be conscious and voluntary, but it cannot be denied that there is a sort of instinctive tendency toward it much as there is in all of us a strong tendency toward a certain orientation to the force of gravity.

The reactions of animals to light have been profoundly modified by the evolution of the image-forming eye. It has been shown by Cole that if an eyeless form such as an earthworm or a form with simple eyes is subjected to stimulation by two sources of light of equal intensity but of different area, the animal is as likely to turn to the smaller light as to the larger one. In forms with image-forming eyes, on the other hand, it is the light of larger area which is the more potent in causing the turning of the body. With the development of image-forming eyes it becomes possible for animals to respond to objects and not to mere differences in the amount of light and shade. The image-forming type of eye is stimulated by a decrease as well as by an increase of illumination on particular parts of its surface. This stimulation is generally associated with an involuntary turning toward the source of stimulation. Hence, the automatic turning of the head toward a new object in the field of vision, and the tendency to follow the movements of bodies with movements of the eyes. The eyes of animals are notoriously quick to respond to movements. The moving thing is the stimulating thing. With the evolution of the image-forming type of eye and the development of acute sensitiveness to change of illumination of particular parts of the retinal surface, the general tendency to go toward or away from light may pass into an involuntary tendency to become oriented toward particular moving objects in the field of vision. When an animal reacts in a definite way to objects impressed on its retina we commonly say that it sees. These reactions to objects come to be very complex and specialized. They come to depend upon the size, form and color of the moving object. But it is not improbable that they have their primary roots in the positive and negative phototaxis of simpler organisms. Josiah Royce in his *Outlines of*

Psychology has gone much farther than I should venture to do, in that he sees in the tropisms a set of tendencies which form a sort of fundamental background even in our own psychology. Objects of our own attention exercise a compelling force over us making us turn toward them. We involuntarily turn toward a person or thing about which we are curious; in fact it requires some voluntary effort not to do so. Is this continual orientation to objects akin to orientation to light, odors, etc., in the lower animals? According to Royce these reactions are fundamentally the same. Perhaps if we should follow the history of behavior closely enough in passing from lower to higher forms we should be able to fill in the intermediate steps. At present the connection is merely a suggestive hypothesis.

Most of the work on tropisms that has been done thus far has consisted in determining the precise way in which tropisms are brought about, and the conditions by which they are modified. To find, as it were, what becomes of the tropisms in the course of mental evolution, how they are converted into higher forms of behavior, is a more difficult task. Voltaire has made the remark that we are governed by instinct as well as cats and goats. It is possible that we may be justified in going somewhat farther than the celebrated skeptic, in saying that to a certain extent we are governed by tropisms as well as insects and worms.

REFERENCES

BOHN, G. (1) La naissance de l'intelligence, Paris, 1909; (2) La nouvelle psychologie animale, Paris, 1911.

COLE, L. J. An experimental study of the image-forming power of various types of eyes. Proc. Am. Acad. Arts and Sciences, 42, 335, 1907.

GEE, W. The behavior of leeches with special reference to its modifiability. Univ. of Calif. Pubs. Zool., 11, 197, 1913.

HOLMES, S. J. (1) Phototaxis in the amphipoda. Am. Jour. Physiol., 5, 211, 1901; (2) The reactions of Ranatra to light. Jour. Comp. Neur. Psych., 15, 305, 1905.

LOEB, J. (1) Der Heliotropismus der Tiere und seine Uebereinstimmung mit dem Heliotropismus der Pflanzen. Würzburg, 1890; (2) The mechanistic conception of life. Chicago, 1912.

LYON, E. P. On Rheotropism. I, Rheotropism in fishes. Am. Jour. Physiol., 12, 149, 1904.

MAST, S. O. Light and the behavior of organisms. N. Y., 1911.

RADL, E. Untersuchungen über den Phototropismus der Tiere. Leipzig, 1903.

ROYCE, J. Outlines of Psychology. N. Y., 1903.

WASHBURN, M. F. The animal mind. N. Y., 1909.

WODSEDALEK, J. E. Formation of associations in the May-fly nymphs Heptagenia interpunctata (Say). Jour. Animal Behavior, 2, 1, 1912.

IV

THE PROBLEM OF ORIENTATION

IN treating of this subject one is compelled to enter a field occupied by contesting parties. The subject of orientation has long been a bone of contention, but it is probable that, as has occurred in so many other controversies, a deeper insight will result from the conflict of opinion. Allusion has been made in the previous chapter to the theory of orientation to light and other forces, which has been developed by Loeb and which has influenced so largely recent work in the behavior of lower organisms. This theory made the orientation of organisms to light, heat, chemicals, etc., and the migration of animals toward or away from the source of stimulus an entirely involuntary response based upon more or less simple reflex action. To construe behavior in terms of tropisms and to explain tropisms as the inevitable effect of reflex action which in turn was supposed to be determined by the mechanical and chemical constitution of the organism formed the general scheme of attack upon problems of behavior which Loeb and his adherents have attempted to follow out. Many features of the behavior of lower organisms were found to receive a very plausible interpretation in accordance with this scheme.

The studies of Jennings on the behavior of the simpler animals revealed many cases of apparent tropisms to which the tropism scheme of Loeb did not apply. Infusorians were found to collect in regions of dilute acid, not because they were oriented to the lines of the diffusing substance, but because when they accidentally swam into the region of the dilute acid they remained there. The collections thus formed were the result of a sort of selection of chance movements. The organisms were found not to be able to orient themselves at all, although the aggregations formed resembled those which in other organisms are the result of orientation.

Although the formation of collections by the infusoria and other asymmetrical organisms may occur without orientation, Jennings believes that in symmetrical forms in which the body of the organism is obviously oriented to the stimulus the process does not occur in accordance with the tropism scheme of Loeb. "In the symmetrical Metazoa," he says, "we of course find many cases in which the animal turns directly toward or away from a source of stimulation, without anything in the nature of preliminary trial movements. This is a simple fact of observation, which leaves open the possibility of many different explanations. Is the simple explanation given by the local action theory of tropisms one that is of general applicability to the directed reactions of lower and higher Metazoa?"

"In considering the evidence on this question, we find that even in the symmetrical Metazoa the direction of movement with reference to external agents is by no means always brought about by a simple, direct turning. On the contrary, in many of the Metazoa, trial movements are as noticeable and important as in the Protozoa. This we have illustrated in detail for many invertebrates in the section devoted to this subject (Chapter XII, Section 2). For such behavior the local action theory of tropisms fails to give determining facts."

Just how Jennings would explain orientation such as occurs when the moth flies into the candle he has nowhere made clear, further than saying that in such cases the organism "reacts as a whole," instead of being oriented by the local reactions of particular organs.

That the orientation of a symmetrical organism may be largely brought about by the indirect method of a sort of trial and error process has been shown, in the case of several organisms, by the present writer. In a paper on the "Selection of Random Movements as a Factor in Phototaxis" I have shown that in earthworms, leeches (Glossiphonia), and the larvæ of blow flies, there is a fairly definite orientation of the body to light rays as the animals move away from the source of illumination, and that it is not so much through a direct turning away from the light that orientation is effected as by the circumstance that all movements, except those bringing the animal away from the light, are inhibited or reversed. If an earthworm is placed at right angles to a beam of light "it will be seen that the head frequently moves from side to side before extension takes place. These movements may be very slight and ordinarily would escape attention. There is often a similar movement during the process of extension. Frequently the head is bent over towards the light during the first part of the extension and bent the other way and extended farther, or again it may be waved back and forth several times. Slight trial movements in all directions are continually being made. The reason why the worm makes more turns of a decided sort away from the light than towards it is largely because the little trials that bring the worm nearer the light are not followed up. Many of the turnings that would naturally be counted as negative are preceded by a slight positive turn followed by a stronger negative one. In order to ascertain whether the negative reaction was manifested at the very beginning of the response, the following experiment was tried: A worm was allowed to crawl on a wet board. When it was crawling in a straight line it was quickly lowered into the beam from a projection lantern so that its body would lie at right angles to the rays. The exposure to the light was made in each case when the worm was contracted, and the first detectible movement of the head to one side noted. In the two specimens employed the first detectible turn was away from the light 27 times and towards the light 23 times. After a few extensions the worm in nearly all cases soon turned and crawled away from the light. The first detectible movement of the earthworm seems, therefore, to be nearly as likely to be towards the light as away from it. The slight preponderance of negative turns may be due to the fact that some of the smaller trial movements were overlooked, to a slight direct orienting effect of the rays, or merely to chance."

In the leech Glossophonia, which crawls by a sort of looping motion, the anterior part of the body is frequently raised, extended, and moved about as if the animal were feeling its way. "If the animal turns it in the direction of a strong light it is quickly withdrawn and extended again, usually in another direction. If the light is less strong it waves its head back and forth several times and sets it down away from the light; then the caudal end is brought forward, the anterior end extended and swayed about and set down still farther from the light than before. When the leech becomes negatively oriented it may crawl away from the light, like the earthworm, in a nearly straight line. The extension, withdrawal and swaying about of the anterior end of the body enable the animal to locate the direction of least stimulation, and when that is found it begins its regular movements of locomotion. Of a number of random movements in all directions only those are followed up which bring the animal out of the undesirable situation."

With the blow fly larvæ the method of orientation was much the same. "When a strong light is thrown on a fly larva from in front, the anterior end of the creature is drawn back, turned to one side and extended again. Often the head is moved back and forth several times before it is set down. Then it may set the head down when it is turned away from the light and pull the body around. If the head in moving to and fro comes into strong light it is often retracted and then extended again in some other direction, or it may be swung back without being withdrawn. If a strong light is thrown on a larva from one side it may swing the head either towards or away from the light. If the head is swung towards the light, it may be withdrawn or flexed in the opposite direction, or, more rarely, moved towards the light still more. If it is turned away from the light the larva usually follows up the movement by locomotion. Frequently the larva deviates considerably from a straight path, but as it continually throws the anterior end of the body about and most frequently follows up the movement which brings it away from the stimulus, its general direction of locomotion is away from the light. In very strong illumination the extension of the anterior part of the body away from the light is followed by a retraction, since in whatever direction it may extend it receives a strong stimulus and the larva writhes about helplessly for some time. Sooner or later, however, it follows up the right movement. Occasionally the larva may crawl for some distance directly towards the light, but after a time its movements carry it in the opposite direction. When once oriented, the direction of locomotion of the larvæ is comparatively straight."

It was not denied that these different forms showed a certain tendency to turn directly away from the light, but it was contended that orientation was mainly produced "indirectly by following up those chance movements which bring respite from the stimulus." The light reactions of the forms studied "may be interpreted as a resultant of two motor responses; first, the activities of locomotion which are set up by the stimulus of the light, and second, the act of jerking back and bending the body from side to side in response to a strong stimulus from in front. Here are two instincts or reflexes, however we may be pleased to call them, which are in a measure antagonistic in that the first is frequently overcome by the second. The direction of the external stimulus determines which of these two instinctive tendencies predominates."

The more recent work of Harper on the earthworm *Perichæta bermudensis* has shown that in strong light the worm turns away from the stimulus, but that in weaker light "orientation is the result of a trial and error method." And Mast on the basis of his studies on the light reactions of another earthworm, Allolobophora, concludes that "selection of random movements, as Holmes, Harper and Jennings pointed out, undoubtedly plays a very large part in the orientation of the earthworm under ordinary conditions." The results obtained by Mast in his careful studies of the reactions of fly larvæ confirm my own position as to the selection of random movements in these forms and add a number of interesting facts, one of which is that under certain conditions orientation may be to a considerable extent direct. Larvæ at first exposed to strong light turn about as often towards as away from it and orientation is effected mainly by the method above described, but after longer exposure the percentage of direct turns from the light increases. This is accounted for by Mast, as follows: "If the larvæ are carefully observed when they are suddenly exposed to lateral illumination by diffuse light, it is found that they respond immediately only if the anterior end is turned toward the source of light when the exposure is made. If this end is in any other position, there is no reaction whatever until the organism, in its normal process of locomotion, extends it toward the source of light. Then it is at once turned from the light to such an extent that it frequently makes a right angle with the posterior end. Later it is swung back, but only part way. The tip is, however, exposed and so the animal may be stimulated again, after which it again turns sharply from the source of light. This process is repeated until the organism has turned to such an extent that the anterior end is practically as much exposed when it turns in one direction as when it turns in the other. The great preponderance of lateral movements from the source of light and direct orientation in diffuse light therefore do not indicate that fly larvæ have the power of differential response to localized stimulation."

Loeb, who sets little store by such proximate categories of explanation as trial and error, has contended against the doctrine that orientation is effected by this method. In speaking of the doctrine that orientation of an organism in strong light may be direct, while in weak light it may take place by the indirect method described above, he says: "If the photosensitiveness of the animal is lessened the animal may deviate for a longer period from the direction of the light rays. Such animals do eventually reach the lighted side of the vessel, but they no longer go straight toward it, moving instead in zig-zag lines or very irregularly. It is therefore not a case of qualitative, but of a quantitative, difference in the behavior of heliotropic animals under greater or lesser illumination, and it is therefore erroneous to assert that heliotropism determines the movements of animals toward the source of light only under strong illumination, but that under weaker illumination an essentially different condition exists."

Now there are undoubtedly forms to which Loeb's remarks are entirely applicable. The possibility of the interpretation which Loeb has given was carefully considered by the present writer while working on the forms above described and was finally rejected as inadequate for the particular cases under consideration. It was pointed out that "a tropism of the direct sort is not necessarily a perfectly fixed and rigid affair. It may be a tendency more or less obscured by a lot of random movements arising from internal causes. An organism may be drawn to a certain point through a direct orienting reflex, but if there is at the same time a large element of random activity in its behavior it may seem to reach that point by the method of trial and error."

A careful consideration of the movements of earthworms, leeches and fly larvæ made it evident that orientation does not take place by the method just referred to. We are not dealing merely with the masking of a simple tropism by a lot of inconsequential activity. It is largely by virtue of and not in spite of random movements that orientation is secured. If an organism were so constituted that whenever it extended toward the light it would jerk back and turn to one side, even though the direction of its turning were totally indeterminate, it would finally become oriented away from the light. To a considerable extent the reactions of the forms described are like those of such a hypothetical organism.

Whatever be the part played by the indirect methods of orientation which have just been discussed, it is evident that very many animals orient themselves by turning directly toward or away from the source of the stimulus. In fact this might be said to be the typical method for symmetrical organisms, and it has been shown to apply to several that are asymmetrical in structure also. Many forms will accurately follow a source of light, changing their direction promptly and without any preliminary trial movements whenever the position of the light is changed. The existence of such behavior is not of course proof of any particular theory of the mechanism of orientation. It is as consistent with the view that light is followed through deliberate volition, or through curiosity as Romanes once suggested, as it is with the reflex theory. The latter interpretation has the principle of Morgan in its favor which is to the effect that "In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty if it can be interpreted as the outcome of one which stands lower in the psychological scale." But the law of parsimony in any of its forms,—and the principle of Morgan is one of them,—never affords proof; it only creates a certain presumption, and one, too, whose strength varies greatly according to circumstances, in favor of any given conclusion.

Several years ago it seemed to me very desirable to study tropisms with the view of testing the possible presence of any more highly developed functions than are postulated by the reflex theory. For some reason this particular quest, which involves one of the most important theoretical considerations connected with the tropism theory, had been almost completely neglected. I have already alluded to some of the initial experiments which consisted in blacking over one of the eyes in several phototactic species of arthropods and then observing their reactions to light under various conditions of exposure. It was found that in several positively phototactic species blinding one eye tended to make the animal perform circus movements toward the normal side. In several negative species similarly blinded, circus movements were performed in the reverse direction. This is what the reflex theory of tropisms would lead us to expect. That the relations discovered are fairly general is evinced by the discovery by other investigators as well as by myself of a number of other forms which react in a similar manner. Great individual variation was found in the degree to which the tendency to perform circus movements was manifested, some forms after being blinded on one side continuing to go toward or away from the light in a nearly straight line. The fact observed by myself in Ranatra and Notonecta and subsequently found by Miss Brundin in Orchestia, that individuals which at first performed circus movements later come to go toward the light in a nearly straight course, indicates a capacity for regulation in behavior if not a primitive form of learning, and suggests the possibility that the normal tropisms of these forms are not wholly a matter of direct reflex action. Were these animals pure reflex mechanisms we should expect their circus movements to continue. But judging from their behavior, these animals follow light more or less after the manner in which higher animals pursue their prey or any other object of interest. Possibly the same may be true of the fiddler crabs which move sidewise toward the light instead of orienting themselves in the usual manner with their longitudinal axis parallel to the rays. Loeb is inclined to the conclusion that "in the fiddler crabs in the first place there is an entirely different connection between the retina and the locomotor muscles from that in other crustaceans, and that, secondly, there is a special peculiarity in regard to the function of the two retinæ whereby they do not act like symmetrical surface elements." In the light of the facts mentioned above it is, I believe, doubtful if we need to assume any far-reaching modifications of nervous structure to account for the peculiar orientation of these crabs. This conclusion is supported, I think, by the experiments of Miss Brundin on *Orchestia traskiana* in which the amphipods which have a narrow compressed body were compelled to travel on one side by being confined between two horizontal glass plates. Although orientation in the usual way was impossible, the amphipods moved toward the light by pushing against the glass with their legs and by flexing and extending the body. The long axis was kept pointed approximately toward the light, but this position was maintained by movements quite different from those involved in orientation under normal conditions. Since the phototaxis of this species is readily modified by experience it is not improbable that something more than direct reflex action is involved. Perhaps the explanation of why animals do the things that they like to do is involved in any complete account of the orientation of higher forms.

For more primitive types in which behavior is little if at all modified through the agency of associative memory there is no reason for doubting that orientation is effected by means of reflex action. But granting this to be true there is room for a variety of ways in which orientation may be brought about. Many animals respond very readily to a sudden change in the intensity of light, while they show little or no response when exposed to constant illumination. In some cases a sudden increase of light intensity produces a reaction, but more frequently the response is evoked when the intensity of the light is diminished. Hungry leeches (Glossiphonia) raise up and extend the anterior end of the body when a shadow passes over them, and mosquito larvæ wriggle downward under the same circumstances. Now organisms of any kind in going to or from the light are subjected to frequent changes of light intensity as they deviate to one side or the other of their course. Do the fluctuations of light intensity so caused produce stimulations that affect the orientation of the animal? The possibility that stimulations produced by such fluctuations in the intensity of light might play a rôle in orientation was suggested in my paper on the phototaxis of Ranatra. As this insect, when one eye is blackened over, nevertheless, in some cases goes nearly straight to the light, it was pointed out that "were the insect so constituted as to respond to an increase of light entering the left eye by a turn to the left and to a decrease of light by a turn to the right, we can understand how, when once pointed to the light, a straight course might be preserved. If the insect turned towards the right there would be an increase of light entering the left eye which we might suppose stimulates the insect to turn in the opposite direction. Deviations to the left would cause a diminution of light entering the left eye, which we might suppose acts as a stimulus to turn to the right side. The right eye may be supposed to act, *mutatis mutandis,* in a similar manner."

The conclusion reached, however, was that responses to fluctuations of light intensity alone did not give an adequate explanation of the orientation of this form, although they might afford a cooperative factor. Such responses probably do play an important rôle in producing those orienting movements known as compensatory motions where the latter are, as in many insects, dependent upon the organs of vision. Mast, who is an opponent of the view that phototaxis is the result of light acting as a constant stimulus, is inclined to attribute orientation very largely to intensity changes. In speaking of orientation in many lower forms, he says: "In many of these forms orientation is undoubtedly, and in all it is probably, a response to change of light intensity on some part of the organism. At any rate it has in no instance been demonstrated that it is, as Loeb states, 'a function of constant intensity,' that orientation to light is like orientation to an electric current." There is much, I believe, that indicates that light stimulates quite apart from the shocks due to variations in its intensity, but the question as to the relative potency of the two factors involved, which Mast has done well to bring into greater prominence, is one that can be answered only by experiment. In the ordinary movements of animals to and from the light both these factors are free to come into play. The natural method of attacking the problem, therefore, is to exclude one of the possible agencies, and then to observe the effect of the other alone.

Recently a series of experiments was carried on by Miss McGraw and myself, in which animals were exposed to illumination which was rendered constant so far as this could be done in the case of an actively moving animal. In one set of experiments the insect was placed in a jar lined below and at the sides with white paper. "This was covered by a cone of the same material in the apex of which was placed an electric light. A small peep hole permitted the observation of the insects in the jar. In several experiments the insect was placed in a small circular glass dish in the center of the enclosure. Whether the insect turned to the right or to the left in this apparatus the amount of light entering the eyes was approximately the same. Insects with one eye blackened over were placed in the jar and stimulated to activity whenever they came to rest by tapping on the jar, or when this failed by poking them with a wire. The very slight variations in the light entering the eye in the different positions of the insect would have different effects, according to the theory of differential sensibility, depending on the position of the insect, and would not tend to produce a constant deviation of the path in any particular direction. The same may be said of variations caused by movements out of the horizontal plane. Since the slight effects of differential sensibility would tend to neutralize one another, any uniformly directed movements may be attributed, with considerable probability, to the constant stimulating effect of the light."

Several negatively phototactic beetles placed in the apparatus showed a general tendency to turn toward the blackened eye. A Jerusalem cricket, Stenopelmatus, which is negative to light, was placed in the enclosure after having its left eye blackened over. When crossing the enclosure it invariably turned to the left and continued to go around in that direction when it came in contact with the edge. Several flies showed very decided circus movements toward the normal side. Thus even under conditions of practically continuous stimulation these forms kept up their orienting activities.

In another set of experiments insects were held in a fixed position while their efforts at locomotion were given opportunity for expression by rotating a horizontal disk mounted on a pivot like the turntable of the microscopist. "The apparatus was made very light and easy running so that even a small insect could set it in motion. By holding an insect over the disk with the head pointing either toward or away from the center, and having a light so that the rays fell on one side of the body, the movements of the legs which would ordinarily turn the insect toward the light would simply cause the disk to rotate in the opposite direction. With the insect held steadily, the stimulus afforded by the light would naturally remain constant, and if light oriented by its constant stimulating effect we might expect that the insect would keep rotating the disk in its attempts at orientation.

"Butterflies proved to be very convenient to work with, since by grasping them by the wings folded together above the body they could be held quite steadily, especially with the aid of a hand rest, above the disk. A cabbage butterfly, *Pieris rapæ,* was held facing the center of the disk and presenting its right side to the light. Almost immediately the butterfly attempted to turn toward the light, and by the action of its legs caused the disk to rotate in the opposite direction. After a few rotations of the wheel the butterfly was turned into the reverse position so that its left side was exposed to the light. Within a few seconds it began to turn the disk away from the light as before. When replaced in its original position the butterfly rotated the disk again toward the left side. Several subsequent trials gave similar results, and another specimen of the same species responded in practically the same way as the one described.

"Experiments with *Melitæa chalcedon* gave results very similar to those with the cabbage butterfly. When the insect was held pointing obliquely away from the light it would still turn the disk away from the more illuminated side. When pointing obliquely toward the light the butterfly would give the same response. In every position except that in which the body was parallel to the rays there were efforts to turn toward the light, which resulted in the rotation of the disk. If the insect was held facing the light, rotary movements were set up as a consequence of attempts at forward locomotion. In many cases the disk would be rotated for several minutes without cessation, and when the butterfly became quiet it could generally be caused to resume its activity by pulling it slightly backwards. In both Pieris and Melitæa the head was kept turned slightly toward the light. *Eurymus eurytheme* and *Cænonympha californica* also rotated the disk away from the light. Most of the specimens of *Euvanessa antiopa* experimented with failed to give results on account of feigning death so long as they were held, but one individual became active after a time and consistently rotated the disk away from the illuminated side.

"Two species of Diptera of the family Tachinidæ rotated the disk uniformly away from the light. Other specimens when held would execute only irregular movements. The same was true of several other phototactic insects belonging to different orders. The aculeate Hymenoptera expended most of their energy in efforts to sting their captor; and attempts to escape in most other cases effectually overcame any phototactic proclivity that may have existed. However, the comparatively few insects that continued to exhibit light reactions under the unnatural condition of being held between the fingers or by forceps gave such uniform and unequivocal reactions that there can be little doubt that light exercised a continuous stimulating influence upon their activity. The slight movements due to one's hand or the insect's own actions would affect but very little the amount of stimulation received by the eye, and whatever effects would be produced would tend rather to neutralize one another than to give rise to any continuous efforts in one direction."

It is not possible, I think, to construe phototaxis entirely in terms of differential sensibility. Responses to the shock due to a sudden increase or decrease of light may play a part in the orientation of many forms, but the continuous stimulating influence of the rays is, in many cases at least, and very probably in most, the factor of greater importance.

The same conclusion is strengthened by the recent excellent investigations of Bancroft on the tropisms of the protozoan Euglena. The phototaxis of this simple organism has been the subject of more or less contention on the part of Jennings, Mast, Torrey, Parker, Bancroft, and to a small extent the present writer, Jennings and Mast having endeavored to prove that orientation takes place by the trial and error method, the other participants maintaining that orientation is direct. Bancroft has shown that orientation is in large measure independent of the reactions to sudden increase or decrease of illumination and that it apparently depends upon a different mechanism. It is not probable therefore that orientation is effected through responses to variations in light intensity as Jennings and Mast have contended.

As Loeb has pointed out if it can be shown that the Bunsen-Roscoe law applies to phototaxis it would make it evident that light acts as a constant stimulus. This law, according to which photochemical effects are proportional to the intensity of light times its duration, has been shown by Blaauw and by Fröschel to apply to the phototropic bendings of several plants, and Loeb and Ewald have shown its application to similar curvatures of the hydroid Eudendrium. As yet the relation of this law to phototaxis in animals has been little studied, owing largely to the practical difficulties of putting it to the test. Inasmuch as light is supposed to stimulate by virtue of the chemical changes it induces in the sensory organs or surfaces of the organism one would scarcely expect to find so general a function as orientation dependent merely on the stimuli afforded by fluctuations of light intensity. Certainly light exercises a fairly constant stimulating effect upon our own eyes, and it is very probable that it acts in much the same way in the lower animals.

REFERENCES

Bancroft, F. W. Heliotropism, differential sensibility, and galvanotropism in Euglena. Jour. Exp. Zool. 15, 383, 1913.

Brundin, M. T. Light reactions of terrestrial amphipods. Jour. Animal Behavior, 3, 344, 1913.

Harper, E. H. Reactions to light and mechanical stimuli in the earthworm Perichæta bermudensis (Beddard). Biol. Bull. 10, 17, 1905.

Holmes, S. J. (1) Phototaxis in the Amphipoda. Am. Jour. Physiol. 5, 211, 1901; (2) The selection of random movements as a factor in phototaxis. Jour. Comp. Neur. Psych. 15, 98, 1905; (3) The reactions of Ranatra to light. l. c. 15, 305, 1905; (4) the phototaxis of fiddler crabs and its relation to theories of orientation. l. c. 18, 493, 1908; (5) The evolution of animal intelligence. N. Y., 1911; (6) Phototaxis in the sea urchin, Arbacia punctulata. Jour. Animal Behavior, 2, 126, 1912.

Holmes, S. J., and McGraw, K. W. Some experiments on the method of orientation to light. Jour. Animal Behavior, 3, 367, 1913.

Jennings, H. S. The behavior of lower organisms. N. Y., 1906.

Loeb, J. (1) Studies in general physiology, Chicago, 1905; (2) Dynamics of living matter, N. Y., 1905; (3) The mechanistic conception of life, N. Y., 1912.

Loeb, J., and Ewald, W. F. Ueber die Gültigkeit des Bunsen-Roscoeschen Gesetzes für die heliotropische Erscheinung bei Tieren. Zent. f. Physiol. 27, 1165, 1914.

Mast, S. O. Light and the behavior of organisms, N. Y., 1911.

Patten, B. M. A quantitative determination of the orienting reaction of the blow fly larva (Calliphora erythrocephala Meigen). Jour. Exp. Zoöl. 17, 213, 1914.

TORREY, H. B. (1) The method of trial and the tropism hypothesis. Science N. S. 26, 313, 1907; (2) Trials and tropisms, l. c. 37, 873, 1913.

WASHBURN, M. F. The animal mind, N. Y., 1909.

V

THE REVERSAL OF TROPISMS

ONE very prevalent and noteworthy peculiarity of the tropic movements of animals and plants is the phenomenon of reversal. The same organism may show a positive or a negative reaction to temperature, light, gravity or the electric current according to the strength of the stimulus, the organism's own condition or the coincident influence of other agencies. Through this power of reversal behavior is rendered more plastic. Granting that the tropisms are involuntary reactions to external stimuli, the fact that the organism may go either toward or away from a stimulus according to how it is influenced by various internal and external conditions makes its behavior much more varied, and affords an opportunity for a closer adaptation to the numerous environmental agencies that affect it.

It is not to be inferred that all reversals of tropisms are adapted to meet some organic need. In many cases nature does not seem to have conferred upon the organism any power of reversal whatsoever. The pomace-fly Drosophila is positively phototactic in very strong light, but Carpenter has shown that when an intensity of 480 candle power is reached the movements of the insect are no longer definitely controlled. The flies tumble and whirl about in an irregular way, but in no case do they show a negative reaction.

There are other cases in which the power of reversal occurs, but where it is not brought into play when it would seem to be most needed. The large terrestrial amphipod or sand flea *Talorchestia longicornis* is ordinarily positive in its reactions to light. When first exposed, especially if it is wet or cold, it may show a vacillating tendency toward the negative reaction, but in strong light, especially in a higher temperature, it becomes strongly positive. I have exposed specimens in a dish one end of which was shaded, while the other was illuminated by direct sunlight. In the strong light they became more strongly positive and persisted in attempting to jump toward the light until they were overcome by the heat and died in a heap at the end of the dish toward the sun. Both the intense light and the heat had the effect of rendering the positive reactions of the creatures more decided.

Similar behavior is shown by the water scorpion Ranatra when it persists in going toward a powerful electric light until overcome by the heat. Such behavior is certainly the reverse of adaptive. Nature has not equipped the Talorchestias and the Ranatras with any method of properly meeting a situation presented by a combination of strong light and a fatal degree of heat. Such combinations are not common in the natural environment of either of these species. Both of them, in common with most other animals, high as well as low, respond negatively in ordinary circumstances to an injurious degree of temperature. Bring a hot needle near either of them and it will turn away. But the remarkably strong proclivity of these forms to go toward the light is sufficient to draw them into a region which they would ordinarily shun. If they turn away at times from the more intense heat their phototaxis quickly brings them back again. They behave as if they were under a powerful spell which they are unable to resist and which they obey as long as any of their vital energy remains.

While there are many animals which cannot be made negatively phototactic by any increase of light, it is not uncommon to find forms that are positive in light of weak or moderate intensity and negative in strong light. Very intense light is often accompanied by an injurious degree of heat and even where it is not, its effects on the organism are probably not good and are sometimes manifestly injurious. The power of change from positive to negative phototaxis in strong light is a serviceable endowment with which we might expect *a priori* to find many organisms equipped. Curiously enough, it is not among the more highly organized phototactic animals that this ability is most widespread. In the insects reversal of the positive reaction is rather uncommon. In the crustaceans reversal in strong light is rather more often found in the more primitive members of the group and in larvæ. Reversal in strong light among the lower invertebrates is fairly common and especially so in the phytoflagellates and other forms which contain chlorophyll or some allied photosensitive substance. The same trait, as Strasburger and others have shown, is frequently manifested by the swarm spores of algæ. In forms containing chlorophyll, light is intimately concerned with the general metabolism, and therefore has an unusually important influence upon organic welfare. Adaptive behavior in relation to changes in light intensity is, in these primitive forms, almost an essential condition of existence.

An excellent illustration of such adaptive behavior is shown by the movements of the chloroplasts in the cells of many plants. It is well known that most green plants bend toward the light so that a great part of their surface may be exposed to the rays. Often the leaves move under the stimulus of light so that the rays impinge upon them at right angles (transverse heliotropism). But in addition to these devices for securing a more effective exposure, another adaptive feature is afforded by the movements of the individual chloroplasts within the cells. These chloroplasts are masses of protoplasm containing chlorophyll. In weak light the chloroplasts are arranged along those sides of the cell at right angles to the rays. When the light is intense, these bodies move to the sides of the cell parallel with the rays where they escape exposure to the stronger stimulus.

A very striking exhibition of similar behavior is shown by the chloroplasts of the filamentous alga Mesocarpus. According to Strasburger, "the chloroplasts in the form of a single plate suspended in each cell turn upon their longitudinal axes according to the direction and intensity of the light. In light of moderate intensity, according to Stahl's observations, they place themselves transversely to the source of light, so that they are fully illuminated (transverse position); when, on the other hand, they are exposed to direct sunlight, the chloroplast plates are so turned that their edges are directed toward the source of light (profile position)." Analogous protection against too strong light occurs in some diatoms in which the chloroplasts when intensely stimulated become aggregated in dense clusters.

Most of the free swimming spores of algæ and a great many of the chlorophyll bearing flagellates keep in situations of optimal light intensity owing to the fact that they are positively phototactic in weak light and negatively so in strong light. The particular intensity of light in which any form tends to remain depends not only upon the species, but also upon various conditions affecting the individual organism. That the organism tends to remain in a region of the most advantageous degree of illumination cannot of course be asserted, especially in view of the many unadaptive features shown by tropic behavior in general, but it is very probable that the region selected represents at least a rough approximation to the optimum.

Intimately related to the effect of intensity of light on phototaxis is the influence of previous exposure. Groom and Loeb in their observations on Balanus larvæ found that these organisms were positive in the morning, even to quite strong light, and that later in the day they became negative, even though the light to which they were exposed became reduced in intensity. That this is not the result of a diurnal rhythm is shown by the fact that positive larvæ placed for a few hours at any time of day in a dark enclosure will be positive when first exposed to light. Similar behavior is shown by *Daphnia magna*, except that in moderate light the animals become indifferent and show a negative reaction when the intensity of the light is increased. After exposure to a stronger light the Daphnias again become indifferent and require a still stronger light to produce a negative response.

The close connection between the influence of intensity of light and time of exposure is shown by the fact that forms that are positive in moderate light frequently do not immediately become negative when strong light is thrown upon them. Strasburger found that the swarm spores of Ulothrix which are positive in weak light remained positive for a very short time when exposed to strong light. Balanus larvæ rendered positive by being kept in darkness swim toward strong light for a short time before they show the negative reaction. The stronger the light the quicker the negative reaction occurs.

In addition to these changes in reaction we have the slower adjustment of many organisms to the continued influence of a particular intensity of light. Adaptations of organisms to stimuli to which they are habitually exposed are common, and the cases of so-called light attunement may be regarded as particular instances of this general process. The diatom *Navicula brevis* is positive only in the weakest light. Verworn exposed a culture of this species to a window for two weeks, after which the diatoms became positive in light to which at first they gave the negative reaction. According to Strasburger the swarm spores of algæ, if kept exposed for a considerable time to relatively strong light, will react positively to a much stronger intensity of light than they did previously. Similar phenomena have been noted by Oltmanns and by Mast in Volvox. Ordinarily the exposure of Volvox to strong light, if not prolonged, has the effect of making the organism negative to light in which it had previously been positive. However, a longer exposure to strong light will have the reverse effect of raising the optimum, the organisms retaining the positive reaction in light which would otherwise have produced a negative response.

From the foregoing facts we may conclude that exposure to light may affect organisms in two different ways. Continued stimulation may render positively phototactic organisms negative. It may also bring about a change of light attunement, thereby dulling the sensitivity of the organism so that it requires a stronger stimulus to evoke a negative reaction. These two opposed results are by no means exceptional phenomena; they are quite parallel to many other physiological changes which render the organism less sensitive to habitual stimuli. The one is a change wrought in the organism as a direct result of the stimulus. The other is a response by the organism, a sort of defensive measure, by which the organism becomes more or less shielded from the action of an inimical force. According to the relative potency of these two modifying factors the effects of previous exposure to light will naturally be varied. Should attunement to increased intensity of light be quickly developed, the effect of continued exposure might appear to make the positive reaction more decided. The effects of exposure to light are notoriously different in different forms, but many of these variations may be the result of the varying potency of the two influences we have discussed.

Exposure in certain cases, however, affects reversal in ways for which it is difficult to account. When studying the light reactions of terrestrial amphipods I discovered that specimens of *Orchestia agilis* which were markedly positive quickly became negative upon diminution of the light. Ordinarily when these forms are placed in a dish and exposed to a window they keep running and hopping in the direction of the light. If now the dish is carried back into a darker part of the room the whole troop of Orchestias will turn about and flock to the negative end of the dish. After being kept for a half hour in the darker part of the room the amphipods again become positive. If they are now carried to a part of the room in which the light is still less intense the negative response appears once more. If the Orchestias are brought back into more intense light they almost immediately become positive again; and the positive reaction appears the more quickly the stronger the light. Usually the transition from weak to strong light causes positive forms to become negative. In the Orchestias we find just the reverse. The transition from positive to negative or the reverse occurs so quickly that it is scarcely possible that change in light attunement plays a part in the transformation.

One might expect, *a priori*, to find tropisms occasionally reversed by temperature, so profoundly does this factor influence all forms of behavior, especially in the lower organisms. Strasburger found that the swarm spores of many algæ are positive at higher temperatures and negative at lower ones. Massart finds that the flagellate Chromulina is positive at 20° C., but negative at 5° C. According to Loeb the larvæ of Polygordius which were negative at 16°

C. became positive when cooled to 6° C. Exceptional individuals which were positive at 17° to 24° became negative at a temperature of 29°. Marine copepods were found by Loeb to be affected in a similar way. Negative specimens of *Orchestia agilis* I have found to be rendered positive much more quickly if the temperature is raised. The same is true for the water scorpion Ranatra. On the other hand, Dr. Dice observed that in *Daphnia pulex* low temperature evokes the positive response. And according to Ewald increase of temperature makes positive larvæ of Balanus negative while decrease of temperature makes negative larvæ positive. Davenport after discussing the effects of temperature on phototaxis states that "All results may be harmonized in the expression: Diminution of temperature below the normal causes reversal of the normal response; elevation of temperature to near the maximum accelerates the normal response." Exceptions to this formula are afforded by many of the larvæ of Polygordius and by certain species of amphipods, both of which are changed from positive to negative at an unusually high temperature. Many forms which are changed from positive to negative by exposure to light are changed more quickly at a higher temperature, but the swarm spores of algæ apparently form an exception to this rule. There are many organisms in which the sense of the phototactic reaction remains the same at all intensities of light, and in these cases temperature usually has no power to reverse the response.

Other tropisms are not so frequently reversed by temperature changes. Parker found, however, that in the copepod Labidocera the females were positively phototactic in warm water and negative in cold, the critical temperature being about 26° C. The geotaxis of the males, like their phototaxis, is weak. Dr. Dice observed that *Daphnia pulex* tends to be positively phototactic at high temperatures and negative at low ones. Several protozoans which are negatively geotactic at ordinary temperatures become positive a few degrees above 0° C., but it may be that in some of these cases low temperature produces a condition of inactivity that leads the organisms to settle at the lower end of their enclosure.

It is a curious fact that the sense of an animal's response to light may be determined by the stimulus of contact with some solid object. Contact stimuli profoundly affect the irritability of many organisms and consequently have a marked influence on their behavior. The instinct of feigning death which is usually elicited as a response to contact and which we have elsewhere suggested is an outgrowth from thigmotaxis, is usually accompanied by a tetanic contraction of the muscles and a reduced sensitiveness to stimulation. It is probably on account of the marked influence of contact upon the physiological states of the lower animals that we sometimes find contact stimuli causing a reversal of the response to light. One of the first cases of this kind was found by Miss Towle in the ostracod crustacean Cypridopsis. Ordinarily negative, this form could be rendered positive by being picked up by a pipette and dropped out again. Often specimens were changed from negative to positive when they collided with the side of the dish. In an allied form, Cypris, Yerkes observed similar changes. Parker, on the other hand, found that in the copepod Labidocera positive specimens could be rendered negative by handling them with a pipette.

The influence of contact on the phototaxis of Ranatra is very marked. Handling this insect throws it into a death feint which inhibits at first all phototactic response, but soon after the creature begins to rouse itself and slowly walk about, it frequently manifests a tendency to slink away from the light. On further exposure this tendency is superseded by the positive response which becomes more decided until the creature is wrought up to a pitch of frantic excitement. Reversal by contact is very clearly shown by this insect if when it is swimming toward the light it is seized and gently stroked, or simply picked up by the tip of the breathing tube and dropped back again into the water. Curiously enough Ranatra does not feign death while in the water, or at least it does not give more than a momentary suggestion of such a performance, but the stimuli which would at once cause it to feign death when in the air, produce an immediate reversal of its phototaxis while in the water.

It is probably owing to the influence of contact that positively phototactic specimens of *Orchestia agilis* become immediately and strongly negative when they are thrown into the water. I have shown that this interesting reversal is not the result of temperature changes or changes in light intensity. It occurs in the same way whether the water is warmer or colder than the air or at the same temperature, and whether there is an accompanying increase or decrease of illumination.

Reversals of tropisms brought about by chemicals are common. Addition to the salt content of sea water was found by Loeb to make negative specimens of Polygordius larvæ and certain copepods positive. Positive specimens of the same forms were made negative by diluting the sea water. Loeb rendered the normally negative Gammarus positive by the addition of carbon dioxide and other acids. Cyclops and Daphnia were rendered positive in the same way. Positive specimens of Diaptomus were found by Moore to be made negative by strychnine, but this negative reaction may be reversed by acids, caffeine, and other substances which ordinarily tend to produce or emphasize the positive response. Ewart discovered that Balanus larvæ were rendered positive by acids, certain salts, and by hypertonic sea water, while alkalies and hypotonic sea water made them negative. Several of my students, Jackson, Michener and Dice who have investigated the problem have shown that there is little apparent relation between the class of chemical used and the influence of the substance on phototaxis. The experiments of Jackson on the fresh water amphipod Hyallella, which is normally negative, have shown that positive phototaxis may be produced by several acids, ammonium hydroxide, and several other chemicals. Michener found in experimenting with a number of diverse forms that if the response is negative it may be rendered positive by chemicals, although positive forms are rarely made negative. Acids, alkalies, salts and various other chemicals of the most diverse sorts would often change the phototaxis from negative to positive. There was a marked similarity of effect produced by chemicals of the most diverse kinds.

While reactions to light may be reversed by many agencies, light in turn may reverse reactions to other stimuli. During the last few years there have appeared several interesting studies on the influence of light and other agencies on responses to gravity. Esterly, in studying the reactions of the copepod Calanus, found that individuals when in the dark became negatively geotactic, but when illuminated either from above or from below they swam downward. Similar behavior was observed by Harper in the larva of the fly Corethra, by Bauer in the crustacean Macromysis, and by McGinnis in the fairy shrimp Branchipus. The recent work of Dr. Dice on the vertical migrations of Daphnia has shown that the changes in the vertical migrations of these forms are not so much the direct effect of reactions to light as the result of the way in which light alters responses to gravity. Daphnias swim upward in the dark, but when illuminated they swim vigorously downward regardless ordinarily of the direction in which light falls upon them.

In many Rhizopods the thigmotactic response is positive to weak contact stimuli and negative to strong ones. Similar relations are found in planarians. Striking cases of the reversal of electrotaxis have been described in a number of diverse types. Volvox, which normally swims toward the cathode, may be caused to swim to the anode by keeping it for two or three days in the dark. Reexposure to light soon brings about the normal response (Terry). Similar reversals of electrotaxis have been observed by Moore and Goodspeed to be produced in Gonium by either acids or alkalies. And Bancroft (1) has shown that Paramœcium, which usually swims to the cathode, may be caused to swim to the anode by various salts of sodium and potassium. Certain salts were found to cause Paramœcium to swim backwards to the anode, a reaction differing from true positive or anodal electrotaxis in that the organisms swim backward instead of forward.

The reader who has had the patience to follow the discussion thus far will appreciate not only how wide spread is the reversal of tropic reaction, but how varied are the causes by which reversal may be produced. Moreover it is difficult to make any generalizations regarding the reversal of tropisms because the same factors often cause quite opposite effects in different organisms. Increase of temperature, as we have seen, may change phototaxis from positive to negative in some forms and from negative to positive in others. Contact stimuli act in the same way as shown by their different influence on the light reactions of Cypridopsis and Daphnia or Ranatra. Exposure to darkness tends to make some species positive and others negative, and exposure to strong light produces similar varied results. These apparently contradictory forms of behavior will probably be reconciled when we have acquired a deeper insight into the physiological mechanisms involved in tropic reactions. Thus far we have had few serious attempts to explain the phenomena of reversal, owing probably to the difficulties and perplexities of the undertaking.

Dr. B. Moore in the course of a paper on the light reactions of certain marine organisms has developed a view which he expresses as follows: "Both the positive and the negative behavior to light may be explained on the basis of one chemical action of the cell (a katabolic one). The positive state indicates that the speed of reactions in the cell lies below a certain value, which may be called the optimal value, and the negative state corresponds to a speed of reactions in the cell above the optimal value. In the former case the sentient surfaces are turned into the light to increase velocity of reaction up towards the optimal value; in the latter case the sentient surfaces are turned away from the light so as to decrease the velocity of reactions down toward the optimal value. As a result of the orientation so caused there arises movement of the organism towards or away from the source of light, but such orientation is not a fixed orientation, but rather a steering action; the animals as a result do not remain in one fixed plane or direction of movement, but the net result of the movement is that the organisms move to or from the light."

This explanation is one that is little more than a statement of the facts to be explained. It is highly probable *a priori* that the speed of reactions in the stimulated cell would increase with the intensity of the stimulus, and to say that when these reactions become sufficiently rapid the sentient surface is turned away tells us no more than that under these conditions the organism becomes negatively phototactic. In Moore's paper there is no recognition of the fact that some organisms are negative when first exposed and tend to become positive the more rapidly in more intense light.

Another interpretation of the reversal of tropisms has been given by Mast (1) in his paper on the light reactions of Volvox. The endeavor is made to correlate the reversal of tropisms with the reversibility of chemical reactions. It is well known that chemical reactions may proceed predominantly in one or another direction according to the amount of substance involved and various external factors, such as temperature and in some cases light. For instance if alcohol is added to acetic acid one will obtain ethyl acetate and water. On the other hand, water added to ethyl acetate results in the formation of alcohol and acetic acid. The reaction in either case does not proceed until all of the original substances are transformed, but only to the point at which certain proportions of alcohol, acetic acid, ethyl acetate and water are reached. This represents the condition of chemical equilibrium. The relative proportions of the compounds present when chemical equilibrium is reached depend upon various external factors. Sometimes one chemical change may occur in the light, while the reverse process takes place in the dark. Under the influence of light the following reaction occurs:

$$2AgCl = Ag_2Cl + Cl,$$

while in darkness there is the reverse change

$$Ag_2Cl + Cl = 2AgCl.$$

Many other compounds, especially the fulgorides, show a similar reversal under different intensities of light. In certain cases chemical reactions are affected in specific ways by the different rays of the spectrum.

"To explain," says Mast, "reversal in the sense of reaction on the basis of chemical reactions induced by light let us assume: (1) That Volvox contains substances X and Y, the chemical reaction between which is regulated by the intensity of light; (2) that a sub-optimum intensity favors the formation of substances represented by X and a supra-optimum those represented by Y; and (3) that the colonies are neutral in reaction when there are Y substances in one member of the equation and X in the other; positive when one member contains (X +) substances and the other (Y —), and negative when one contains (X —) and the other (Y +)." Volvox is positive in weak light and negative in strong, but when placed in light of supra-optimal intensity it does not immediately change its response. This, as Mast suggests, may be due to the fact that some time is required to transform the substance X upon which the positive reaction is supposed to depend. After more of Y was produced and the amount of X diminished through the action of more intense light the negative reactions would be initiated.

This interpretation, which is confessedly very speculative, not improbably contains elements of truth. It is probable that reversible chemical reactions effect the general restoration of organic equilibrium which had been disturbed by the influence of the stimulus. Whether positive and negative phototaxis depend on the relative proportions of the substances belonging to a single equation is of course very problematical. It might be that the formation of a substance A which is favored by intensity of light brings about a negative reaction, while the positive reaction might depend upon the formation of another substance B which was not connected with

A at all. We are warranted in assuming that the ability to respond to light depends upon the existence of substances that undergo photochemical changes. The effect of light would be to exhaust certain substances and to cause the accumulation of their products. These products when they exist in a certain degree of concentration may stimulate directly or indirectly (possibly through their influence on oxydative processes) certain locomotor mechanisms, while at a lower degree of concentration other mechanisms may be more stimulated. It may not be necessary to make any particular assumptions concerning the rôle of reversible chemical reactions, although the fact that such reversibility is a general property of chemical changes is naturally involved in any explanation of recovery from the effects of stimulation, and indeed in the interpretation of many other vital phenomena.

To give a concrete illustration of how reversal may occur according to the preceding interpretation let us consider the reactions of Planaria to weak and strong mechanical stimuli. It has been shown by Pearl that *Planaria maculata* reacts positively to very weak mechanical stimuli, and in fact to very weak stimuli of many kinds, while to strong stimuli it gives the negative reaction. The positive response is brought about by the contraction of the longitudinal muscles near the stimulated point. In the negative response the planarian turns away, not like a higher animal by the contraction of the muscles of the opposite side of the body, but by an actual lengthening of the stimulated side. This lengthening is probably effected by the contraction of the dorso-ventral muscles which run from the dorsal to the ventral body wall, and possibly also by the circular muscles. The response is local and near the stimulated area as it generally is in the lower invertebrates. The positive and the negative reactions depend either upon the functioning of two quite distinct reflex arcs, or, in case the afferent impulses travelled in the same path, upon the diversion of the stronger stimulus into a new pathway. It is well known that strong stimuli often break over into additional pathways of discharge, and it is of course possible that such a phenomenon might occasion a reversal of reaction.

What part the inhibitory influence of stimuli may play in reversal is uncertain. Loeb has alluded to the possible rôle of this factor in one of his earlier papers ('93), but without developing the suggestion further. When an earthworm turns away from the light we may assume, as in fact has been done by Davenport ('97), that the action of the muscles on the more illuminated side is inhibited, and that the animal accordingly turns away from the stimulus. There is no evidence, however, that such an inhibitory process occurs. A worm turns violently away when one side is touched with a hot needle, but the movement is not due to the mere inhibitory effect of the stimulus. If the turning away from the hot needle is due to the contraction of the longitudinal muscles of the opposite side of the body one would naturally suppose that the avoidance of a light was brought about in the same way.

A few years ago I endeavored to study the possible inhibitory effect of light in the phototaxis of Volvox. If the orientation of Volvox when swimming toward the light is due to the fact that light tends to inhibit the action of the flagella on the more strongly illuminated side, we should expect that, as the organism passed from a region of dim light to where the light was more intense, its general rate of locomotion would decrease, since both sides would be more strongly affected by the inhibitory stimulus. Specimens of Volvox were placed in a glass trough the bottom of which was marked off into equal spaces. The time required for a specimen to traverse each space in its course toward the light was noted in a number of cases, and it was found that, on the average, the speed of the organism was quite uniform in the varying intensities of light. The Volvox swam with much the same rapidity until they came near the optimum when their pace began to slacken. The results of the experiments were therefore opposed to the view that orientation is effected by the inhibitory effect of light on the movements of the flagella on the more illuminated side of the organism. Inhibition may function in other ways in the orientation of Volvox and in changing the sense of its reactions to light and other forms of stimulation. There is much to indicate that inhibition is intimately related to reversal of tropisms in many forms, but I shall not venture upon any speculations, which at best could only be very tentative, as to its method of operation.

It is quite possible that the explanation of reversal of tropisms may be quite different in different cases. Many rhizopods show a positive thigmotaxis to a weak mechanical stimulus, while they give a negative reaction if the stimulus is strong. Is this to be explained in the same way as the reversal in the beat of the flagellum in a flagellate, or of the cilia in an infusorian? And does any of these cases have anything in common with the reversal of tropisms in an insect or worm? The mechanism of orientation is quite different in different organisms, and it seems not improbable that the inner mechanism of reversal may be very different also, although there may be broad underlying features common to numerous apparently different cases.

Up to the present time most of the work on the reversal of tropisms has been done with a view of ascertaining the various conditions under which reversals may occur. Many interesting facts have been accumulated, but, as we have seen, they afford no very sound basis for generalization. We shall make little further progress by mere induction. We need to feel our way along by making hypotheses and testing them by appropriate experiments. But when one attempts to attack the problem in this way he soon finds himself hampered by the paucity of knowledge in those fields to which he would naturally turn for helpful suggestions. It would be very desirable to have a more adequate knowledge of the inner mechanism of orientation. It would be very helpful to have a deeper insight into the physiology of irritability. We know little of the processes covered by the word stimulation. We are still looking for a satisfactory explanation of the curious phenomenon of inhibition. The behaviorist may discover many facts of interest and value regarding the reversal of tropisms, but before arriving at an adequate explanation of this perplexing phenomenon he may have to wait until some of the more general and fundamental problems of irritability have been solved.

REFERENCES

BANCROFT, F. W. (1) The control of galvanotropism in Paramœcium by chemicals. Univ. of Calif. Pubs. Physiol. 3, 21, 1906; (2) Heliotropism, etc., in Euglena. Jour. Exp. Zool. 15, 383, 1913.

BAUER, V. Ueber die reflektorische Regulierung der Schwimmbewegungen bei den Mysideen, etc. Zeit. allg. Physiol. 8, 343, 1908.

BOHN, G. La naissance de l'intelligence. Paris, 1909.

DAVENPORT, C. B. Experimental Morphology. N. Y., 1897-99.

Dice, L. H. The factors determining the vertical movements of Daphnia. Jour. Animal Behavior, 4, 229, 1914.

Esterly, C. O. Reactions of copepods to light and gravity. Am. Jour. Physiol., 18, 47, 1907.

Ewald, W. F. On artificial modification of light reactions and the influence of electrolytes on phototaxis. Jour. Exp. Zool., 13, 591, 1912.

Groom, T. T. and Loeb, J. Der Heliotropismus der Nauplius von Balanus perforatus und die periodischen Tiefenwanderungen pelagischer Tiere. Biol. Cent., 10, 160, 1890.

Harper, E. H. Behavior of the phantom larva of Corethra plumicornis. Jour. Comp. Neur. Psych., 17, 435, 1907.

Holmes, S. J. (1) Phototaxis in the Amphipoda. Am. Jour. Physiol., 5, 211, 1901; (2) Phototaxis in Volvox. Biol. Bull., 4, 319, 1903; (3) The reactions of Ranatra to light. Jour. Comp. Neur. Psych., 15, 305, 1905; (4) The reactions of mosquitoes to light in different stages of their life history. Jour. Animal Behavior, 1, 29, 1911.

Jackson, H. H. T. The control of phototactic reactions in Hyalella by chemicals. Jour. Comp. Neur. Psych., 20, 259, 1910.

Loeb, J. Ueber künstliche Umwandlung positiv heliotropischer Tiere in negativ heliotropische und umgekehrt. Arch. ges. Physiol., 54, 81, 1893.

Mast, S. O. (1) Light reactions in lower organisms. II. Volvox globator. Jour. Comp. Neur.

Psych., 17, 99, 1907; (2) Light and the behavior of organisms. N. Y., 1911.

McGinnis, M. O. Reactions of Branchipus serratus to light, heat and gravity. Jour. Exp. Zool., 10, 227, 1911.

Moore, A. R. (1) Concerning negative phototropism in Daphnia pulex. Jour. Exp. Zool., 13, 572, 1012; (2) Negative phototropism in Diaptomus by means of strychnine. Univ. of Calif. Pubs. Physiol., 4, 185, 1912.

Moore, B. Observations of certain marine organisms of (a) variations in reaction to light, and (b) diurnal periodicity of phosphorescence. Biochemical Jour., 4, 1, 1909.

Parker, G. H. Reactions of copepods to various stimuli and the bearing of this on their daily depth-migrations. Bull. U. S. Fish Comm., 21, 103, 1901.

Pearl, R. The movements and reactions of fresh-water planarians. Quart. Jour. Mic. Sci., 46, 509, 1903.

Strasburger, E. Die Wirkung des Lichtes und der Wärme auf Schwärmsporen. Jen. Zeit. n. F. 5, 572, 1878.

Terry, O. P. Galvanotropism of Volvox. Am. Jour. Physiol., 15, 235, 1906.

Towle, E. A study in the heliotropism of Cypridopsis. Am. Jour. Physiol., 3, 345, 1900.

Verworn, M. General physiology. London, 1899.

YERKES, R. M. Reactions of entomostraca to stimulation by light. II. Reactions of Daphnia and Cypris. Am. Jour. Physiol., 4, 405, 1901.

VI

THE BEGINNINGS OF INTELLIGENCE

NOTHING shews more the force of habit in reconciling us to any phenomenon, than this, that men are not astonish'd at the operations of their own reason, at the same time, that they admire the *instinct* of animals, and find a difficulty in explaining it, merely because it can not be reduc'd to the very same principles. To consider the matter aright, reason is nothing but a wonderful and unintelligible instinct in our souls, which carries us along a train of ideas, and endows them with particular qualities, according to their particular situations and relations.—David Hume, *Treatise on Human Nature.*

We all have a certain curiosity regarding the evolutionary history of our various powers and attributes, but from many points of view an unusual interest attaches to the first development of intelligence. The word intelligence is used in a variety of senses by writers on comparative psychology, and any discussion of the origin of intelligence would be fruitless unless the meaning in which the term is employed be understood. One of the foremost of comparative psychologists, the acute Father Wasmann, defines intelligence as "the power of conceiving the relation of concepts to one another and of drawing conclusions therefrom. It involves abstraction, deliberation and self-conscious activity." Intelligence, according to Wasmann, is the God-given attribute of man alone; its possession separates man from brute by an impassable barrier.

Many comparative psychologists, among whom we may mention Lloyd Morgan, Forel and Loeb, adopt as a criterion of intelligence the power of forming associations, or associative memory, and we shall follow the usage of these writers. It is obvious that the possession of this faculty marks an important step in advance upon the creatures whose actions are fatally determined by their instinctive make-up. From its beginning in forms in which the simplest associations are established only after a large number of experiences, intelligence has assumed a rôle of ever-increasing importance in the evolution of animal life, until in man, who is notoriously a weakling compared with the large beasts with which he has had to contend, it became the main factor to which the human species owes its supremacy in the struggle for existence.

In considering the origin of intelligence one is naturally led to the subject of the relation of intelligence to instinct. Formerly it was the custom to contrast these two faculties as if they represented diametrically opposed types of activity. Instinct was regarded as something unalterably fixed, machine-like and practically perfect in its adaptation to the needs of the animal; intelligence was recognized as the antithesis of all these qualities—variable, plastic and eminently fallible. With the establishment of the theory of evolution writers became more disposed to discover the kinship and filiation of instinct and intelligence and they have given us a variety of views as to the relation of these faculties.

Basing his theory on Lamarck's doctrine that instinct is inherited habit, G. H. Lewes attempted to explain instinct as "lapsed intelligence." Performances which are learned with difficulty come, after sufficient repetition, to be carried out automatically and without any intelligent guidance. If the acquired facility of performing these acts is inherited and the acts are repeated generation after generation, it is probable that they might finally be performed by an individual without any previous instruction at all; that is, they would become instinctive. An animal's instincts, according to this view, represent the stereotyped and mechanized behavior which its ancestors found to be profitable; their adaptiveness rests upon the wisdom acquired by ancestral experience. More recently this view has been upheld by Eimer, and in a less extreme form by Romanes, Wundt and many others.

One difficulty with the theory of lapsed intelligence is that it involves the acceptance of the doctrine of the transmission of acquired characters, which has come to be a very questionable biological theory. But another and more fundamental difficulty is revealed by recent work on the behavior of lower organisms. If instinct were derived from intelligence by a sort of mechanizing process we should expect, as Whitman has urged in his criticism of Lewes's theory, to find intelligence dominant in lower forms of life, and that acts which are instinctive in the higher animals would be intelligently performed by the lower ones. The work that has been done on the behavior of lower organisms enables us to state with confidence that such is not the case. In several large phyla of the lower invertebrates there has not, as yet, been demonstrated the least glimmer of intelligence; and, as we pass up the scale of life, intelligence gradually supersedes instinct, not the reverse. We can say with some degree of assurance that, however the transition may have been effected, intelligence has grown out of purely instinctive behavior.

It is not possible, however, to fix, except with the rudest approximation, the stage of evolution at which intelligence makes its first appearance. The transition from instinct to intelligence has been made, in all probability, not once, merely, but several times along different lines of descent. Intelligence in the vertebrates doubtless arose independently from that of the insects, and the intelligence exhibited here and there among the mollusks probably arose independently along a third line of development. Intelligence makes its appearance at a certain stage of organization along whatever line such a stage may have been reached.

Up to the point at which the power of associative memory becomes manifest there has been progress along many lines which has prepared the way for the evolution of this new faculty. Behavior has not only become more complex, but it has become more plastic and capable of easy modification to suit new conditions. The lower organisms do not always react in a particular way to a given stimulus. What reaction occurs may depend upon the number of previous stimulations, the supply of food, exposure to different environing conditions, and numerous other factors which influence the internal state of the organism. The behavior of many lower animals is plastic and adaptive to a remarkable degree, and to a superficial consideration often gives the appearance of a considerable degree of intelligence, without there being any detectable power of associative memory. This plastic and varied behavior not only simulates intelligence, but it secures for the organisms many of the advantages which intelligence confers. It adapts the animal to a more varied environment, and gives it the power of meeting a given situation in more than one way, so if one kind of response does not suit, another may be more successful. Let us glance briefly at some of the ways in which behavior may be modified.

A very general change of behavior in organisms consists in the habituation to any stimulus which is repeated at sufficiently close intervals so that the organism no longer responds to it. This is shown even among the protozoa. A Stentor or a Loxophyllum subjected to a light mechanical stimulus at short intervals soon fails to respond as at first, but the duration of the modification so produced is very short; in Loxophyllum it probably does not extend over two or three seconds. Similar effects of repeated stimulation but of longer duration have been observed in Hydra, several species of sea-anemones, planarians, annelids and various other lower invertebrates. As a rule failure to respond may occur more quickly and the effects of the stimulus remain longer as we pass up the scale of animal life.

Occasionally the reverse phenomenon occurs when the response to a given stimulus is increased instead of diminished with repeated applications—a result which suggests the effect of the summation of stimuli. At times, as Bohn found in Cerianthus, there is an initial increase of responsiveness followed by a dulling of sensitivity. Bohn has attempted to subsume the effects of repeated stimulation under a general "law" to the effect that stimulation always produces at first increase of sensitivity to be followed later by a decrease. Sometimes, as Bohn claims, the initial increase is so short as to escape detection; which may be true, but the burden of proof is on M. Bohn.

Repetition of a stimulus may call forth not only quantitative differences of response, but it may evoke responses of very different character. Animals are frequently provided with several modes of reacting to a given stimulus which may be called into play one after the other. Jennings has shown that if a Stentor is subjected to a light mechanical stimulus by causing fine particles of India ink to fall upon its disk from a capillary pipette it usually reacts first by bending a little to one side. If the particles continue to fall on the disk the beat of the cilia covering the body may suddenly be reversed, thus creating a current tending to carry the offending particles away. If in spite of this the particles still impinge upon the disk the Stentor may contract one or more times. Finally, if all these reactions are tried in vain the infusorian may give a number of violent contractions, break loose from its place of attachment, and swim away.

It would be an error to interpret the varied behavior of this unicellular organism as a manifestation of intelligence, although it is not unlike what the behavior of an intelligent creature might be under the circumstances. No power of learning by experience has ever been discovered in Stentor, or indeed in any other protozoan. The organism is provided with a number of different modes of response, and which one is set in action depends upon internal factors which are influenced by the creature's previous activity. The organism which has responded to a stimulus has become transformed into a different mechanism which may respond more or less readily than before or radically change its method of behavior.

A striking illustration of varied responses to a given stimulus has been described by Jennings in the sea anemone Stoichactis. If a foreign body is placed upon its disk the anemone tries to rid itself of the object in various ways. The tentacles near the object collapse and the area between them extends, thus producing a relatively smooth surface so that the waves can readily wash the object away. If this does not occur the region under the object begins to swell, thus rendering the removal of the object still easier. If this reaction is unsuccessful the edge of the disk begins to sink so that a smooth sloping surface is formed from which the object can readily slide. Here, as in the case of Stentor, we have an organism capable of reacting in several ways to a given stimulus. What particular reaction is evoked depends upon previous stimulations.

Modifications of behavior caused by different conditions of nutrition are found in the lowest members of the animal kingdom. Even the white blood cells after they have ingested a number of bacteria refuse to take in more. Whether there is a limit to the appetite of Amœba has not been determined, but many infusorians such as Stentor, after having swept in a certain amount of food, react to food particles in a quite different way than when in a hungry condition. Hydra when not fed for some time extends the body, sways about in various directions and keeps up a restless movement of its tentacles, thereby increasing its chances of contact with the small creatures which serve as its prey.

Instances of the non-intelligent modifications of behavior might be multiplied indefinitely. As we pass to higher forms the capacity for responding in different ways to a given situation becomes greatly increased. "Nature," says James in his admirable chapter on instinct, "implants contrary impulses to act in many classes of things, and leaves it to slight alterations of the conditions of the individual case to decide which impulse shall carry the day," and he points out that many animals lose the instinctive demeanor and appear to lead a life of hesitation and choice, not because they have no instincts, but because they have so many of them that they block one another's path. Intelligence in the acceptation of the term which we have adopted begins with the formation of associations. It does not make its appearance, so far as is known, until a comparatively high stage of organization has been attained. The evolution along the lines of complexity of instinct and ready modifiability of reactions to suit new conditions, affords a substantial basis for intelligent behavior. Without such evolution the power of associative memory would avail little. But with a large number of readily modifiable instincts, associative memory becomes the means of affording a much wider and closer adjustment to the environment.

The studies which have been made of primitive types of intelligence such as found in crustaceans, fishes and amphibians have shown that associations are formed by a gradual process of reinforcement or inhibition of a particular reaction to a given stimulus. The method followed is one which Lloyd Morgan has designated as "trial and error." It may be illustrated by the experiment of Yerkes on the formation of associations in the crayfish. In these experiments a box was employed into one end of which the crayfish was admitted through a narrow aperture. The other end of the box was divided by a median partition which gave the crayfish a choice of two routes to a tank of water at the other end into which the creature was naturally desirous of getting. One of the two ways to the water was closed by a glass plate at its farther end so that the crayfish was afforded a choice of a right and a wrong path to the water. Would the crayfish after a number of trials learn to choose the right path and avoid the closed passage? In the first ten experiments the crayfish went as often to the right as it did to the left, but in the next ten trials the percentage of correct choices was somewhat greater. Finally after a large number of trials the animal came to choose the right path to the water, making but rarely any mistakes.

Similar experiments with crabs, fishes and the frog have yielded similar indications of slow learning. In some respects such learning resembles the slow formation of a habit rather than the judgment of a consciousness which "sizes up" the situation and determines upon a certain course of action. It is quite probable that such a primitive form of learning does not include any association of ideas. It can be satisfactorily accounted for by assuming nothing more than an association of certain sense perceptions with particular movements. The animal may have no ideas to associate—nothing but sense impressions and motor impulses. Of course its mental content *may* include much more than this, but in interpreting the behavior of animals it is generally advantageous to follow the principle laid down by Lloyd Morgan—which is a sort of special application of the law of parsimony—that we should not assume the existence of a higher psychic function if the phenomena can be explained as well in terms of a lower one.

The step from sensori-motor association to the association of ideas is not, I believe, a wide one, and comes about as a natural consequence of the elaborateness and what Hobhouse has designated as the "articulateness" of the mental process of adjustment. It is foreign to our purpose, however, to trace the increase in the number, delicacy, quickness and complexity of the processes of association which we meet in the various stages of mental evolution. Our problem at present lies in the initial step involved in the formation of a simple association. And it is a problem which, despite its apparent simplicity, involves the consideration of some vexed and subtle questions.

In learning we have to do with two opposite processes of reinforcement and inhibition. A chick after it pecks at a caterpillar which is wholesome and savory pecks at a similar caterpillar more readily on a second occasion. Something has apparently reinforced the connection between the visual impression produced by the caterpillar and the pecking impulse. If, on the other hand, the chick pecks at a caterpillar having a nasty taste it is apt to avoid pecking at it a second time. Something has happened to inhibit the response that would otherwise occur. We commonly explain such behavior by ascribing to the creature feelings of pleasure and pain. We say that the chick pecks at one kind of a caterpillar because of the pleasant taste it derives, and avoids another variety because its taste is bad. Pleasure and pain apparently function as agents for the reinforcement of certain reactions and the stamping out of others. It is a general rule, though not without certain exceptions, that what affords pleasure is conducive to organic welfare, while that which is productive of pain is injurious. The upshot is that the associations that are the outcome of the pleasure-pain response are of just the kind that minister to the animals' needs. Beneficent arrangement! Apparently we have to do with a selective agency which preserves and intensifies certain kinds of behavior and rejects others on the basis of their results—a kind of "sorting demon" in the realm of behavior. What could be more teleological!

The fact that what is pleasant is usually beneficial and what is painful is usually injurious may be explained with some plausibility as the result of natural selection, as was first contended by Herbert Spencer. Animals which took pleasure in doing things which were bad for them and which experienced pain in doing things which were good for them would be very apt to fare ill in the struggle for existence. Natural selection would ever tend to bring about a condition in which the pleasant means the organically good and the painful means the reverse. We should not expect the correspondence, if brought about in this way, to be complete, and it is rather in favor of the theory that we do not find it so.

But granting this contention of Spencer, there is the important question still left unanswered, namely, Why do animals follow what is pleasant and avoid what is painful? In other words, why does pleasure reinforce and why does pain inhibit? Here is another fundamental problem and we find that Spencer with his usual appreciation of fundamental problems was on the ground early with a theory. Pleasure, according to Spencer, is the concomitant of a heightened nervous discharge; pain the concomitant of a lessened nervous discharge. An act which brings pleasure causes an influx of nervous energy to the centers concerned in the movement; the lines of discharge become "more permeable," and upon a repetition of the conditions the same act follows with greater readiness than before. If the act is followed by pain with its concomitant of lessened nervous discharge, the diminution of nervous energy serves to prevent the performance of the act in response to the same conditions. Closely similar explanations of the physiology of the pleasure-pain response have been given by Bain and by Baldwin, the latter declaring that "pleasure and pain can be agents of accommodation and development only if the one, pleasure, carry with it the phenomenon of motor excess—and the other, pain, the reverse—probably some form of inhibition or of antagonistic contraction."

The physiological concomitants of pleasure and pain have afforded a subject for numerous laboratory studies and almost no end of theories. It has been impossible thus far to discover that either of these states is invariably accompanied by any definite physiological condition. The theory of Spencer and Bain is open to obvious criticism, for the man who steps on a tack undoubtedly has a "heightened nervous discharge," as much as a man who shouts for joy. And I believe I am safe in saying that no theory of the physiology of pleasure and pain is on a sufficiently firm basis to warrant its being regarded as anything more than a very tentative working hypothesis.

With our present knowledge of the psycho-physiology of pleasure and pain, the attempt to explain how these states or their physiological concomitants, whatever they may be, can act as agents of reinforcement and inhibition seems rather a fruitless one. The process which we meet at the beginning of intelligence in simple associative memory may be formulated as follows:

stimulus—reaction—pleasure—reinforcement
physiological state *x*
stimulus—reaction—pain—inhibition
physiological state *y*

Spencer, Bain and others have endeavored to show how the organic accompaniments of pleasure and pain modify the creatures' subsequent responses. But as the problem was interpreted by these writers our ignorance concerning the physiological states *x* and *y* brings us to a standstill.

In his valuable work on *Mind in Evolution* Hobhouse has presented a new point of view in considering this problem, which has the advantage of not involving any general theory of the physiology of pleasure and pain. It is essentially a theory of how behavior comes to be adaptively modified through the formation of associations. It makes no attempt to explain why pleasure is associated with certain experiences and pain with others. Such association may turn out to be as inexplicable as the problem why stimulation of the optic nerve gives rise to a sensation of light instead of some other kind of feeling. What it is feasible to attempt to explain is why certain responses tend to be repeated and others tend to be inhibited. And this can be explained with some plausibility as due to the congruity or incongruity of the reactions which come to be associated. For the sake of illustration let us consider again the chick which pecks at a nasty caterpillar. The irritation set up by the caterpillar in the chick's mouth evokes movements of withdrawal and ejection. The two responses of pecking and ejection become associated, but as the two movements are contradictory the result is inhibition. The pecking reaction no longer occurs in the presence of a second nasty caterpillar, not because of any stamping-out influence of the physiological concomitant of pain, but because it becomes joined with an antagonistic reaction.

In a previous paper by the writer the attempt was made to extend the theory of Hobhouse to account for the reinforcement commonly held to be caused by pleasure. The assumption was made that this process is due to an organic congruity of the reactions. If the caterpillar pecked at is a savory one there is set up the reflex of swallowing. Pecking and swallowing form the normal elements of a chain reflex; when one part of the structure concerned is excited it tends to increase the tonus of the associated parts, and thus reinforce the original response. I have found that in the crayfish stimulation of the antennules, which are important organs of smell, sets up chewing movements of the mouth parts and grasping movements of the small chelæ. Similarly stimulating the small chelæ evokes chewing movements of the mouth parts and twitching of the antennules, while stimulating the mouth parts directly may cause movements in both the other sets of organs. We have here as a matter of fact a number of reflexes which mutually reinforce one another. Suppose that in the chick the sight-pecking response and the taste-swallowing response are related as the feeding reflexes demonstrably are in the crayfish; the second response would thus tend to reinforce the first, and if this tendency persisted we would have a case of learning by experience.

Animals in the course of their instinctive responses encounter stimuli which bring about other responses. These become associated. According to the nature of the nervous pathways involved, there may be reinforcement of, or interference with the original reaction. Experience brings about an extension of the range of adaptations by the assimilation of congruent reactions and the elimination of acts whose secondary consequences are in the nature of antagonistic and thereby inhibitory responses. Such we may say, by way of expressing a tentative viewpoint, is the nature of primitive intelligence.

But it will be seen that the capacity to form new adaptations rests upon the primary adaptiveness of the instinctive reactions. The power of formation of associations alone would never lead to improvement. The adaptiveness of intelligence is based upon the adaptiveness of instinct; it may be said that intelligence is a means of enabling an animal to live its life more completely and successfully, but instinct furnishes the fundamental springs of action. Even complex creatures like ourselves form no exception to this rule.

REFERENCES

Bain, A. The senses and the intellect. 3d ed., 1894. The emotions and the will, 4th ed., 1899.

Baldwin, J. M. Mental development. Methods and processes. 2nd ed. N. Y., 1903. Development and evolution. N. Y., 1902.

Bohn, G. La naissance de l'intelligence. Paris, 1909.

Hobhouse, L. T. Mind in evolution. London, 1901.

Holmes, S. J. (1) Pleasure, pain and the beginnings of intelligence. Jour. Comp. Neur. Psych. 20, 145, 1910. (2) The evolution of animal intelligence. N. Y., 1911.

JENNINGS, H. S. (1) Contributions to the study of the behavior of lower organisms. Carnegie Inst. Pubs., 1904. (2) Modifiability in behavior. I, Behavior of sea anemones. Jour. Exp. Zool. 2, 447, 1905. (3) Behavior of lower organisms. N. Y., 1906.

SPFNCER, H. Principles of psychology. N. Y., 1892.

WASMANN, E. Instinct and intelligence in the animal kingdom. St. Louis, 1903.

WHITMAN, C. O. Animal behavior. Biol. Lectures, Marine Biol. Lab., Woods Hole, 1898.

VII

SOME CONSIDERATIONS ON THE PROBLEM OF LEARNING

THE essential nature of the process of learning constitutes a problem of such fundamental importance for psychology, to say nothing of physiology also, that any discussion which promises to contribute anything, however little, toward its solution is abundantly justified. In the previous chapter an interpretation of the process of learning was briefly outlined, and it may be profitable to consider here some other proposed solutions of the same problem, as well as certain criticisms of the view set forth in the preceding pages. The formulation and criticism of different hypotheses regarding the mechanism of learning is especially desirable, since the pathway ahead is none too clear, and since we have to rely to a large extent upon the method of trial and error in order to make progress.

An ingenious explanation of the learning process has been put forward by Thorndike,[1] who, like Spencer and Bain, finds the explanation of the reinforcement and inhibition of reactions in the pe-

[1] "Animal Intelligence." The Macmillan Co., N. Y., 1911.

culiar physiological processes supposed to accompany the satisfying and annoying experiences of the animal. Thorndike recognizes that while the tendency of animals to repeat responses that bring satisfaction or pleasure and to discontinue responses that entail pain usually leads to advantageous results, this rule is not without its exceptions. "Many animals are satisfied by deleterious conditions. Excitement, overeating, alcoholic intoxication are, for instance, very potent satisfiers of man," and conditions which are very salutary often fail to produce satisfaction, and may even bring positive displeasure. All this is simply a matter of imperfect adjustment. "Upon examination," says Thorndike, "it appears that the pernicious states which an animal welcomes are not pernicious *at the time, to the neurones.* We learn many bad habits, such as morphinism, because there is incomplete adaptation of all the interests of the body-state to the temporary interest of its ruling class, the neurones. So also the unsatisfying goods are not goods to the neurones at the time. We neglect many benefits because the neurones choose their immediate advantage. The neurones must be tricked into permitting the animal to take exercise when freezing or quinine when in a fever, or to free the stomach from certain poisons.

"Satisfaction and discomfort, welcoming and avoiding, thus seem to be related to the maintenance and hindrance of the life processes of the neurones rather than of the animal as a whole, and to temporary rather than permanent maintenance and hindrance."

Now the modification of behavior through changes in the neurones is concerned chiefly with what affects the permeability of certain lines of communication in the nervous system. The seat of these changes in permeability is thought by many physiologists to reside in the synapses or membranes between the ends of anastomosing processes of the nerve cells. While the experimental evidence for this conclusion is rather meager we may adopt it provisionally as perhaps the most plausible view at the present time. The condition which permits the ready transfer of impulses from one neurone to another Thorndike calls the "intimacy of the synapse," and he formulates the following provisional hypothesis to account for the process of learning: "A neurone modifies the intimacy of its synapses so as to keep intimate those by whose intimacy its other life processes are favored and to weaken the intimacy of those whereby its other life processes are hindered. The animal's action-system as a whole consequently does nothing to avoid that response whereby the life processes of the neurones other than connection changing are maintained, but does cease those responses whereby such life processes of the neurones are hindered.

"This hypothesis has two important consequences. First: Learning by the law of effect is then more fully adaptive for the neurones in the changing intimacy of whose synapses learning consists, than for the animal as a whole. It is adaptive for the animal as a whole only in so far as his organization makes the neurones concerned in the learning welcome states of affairs that are favorable to his life and that of his species and reject those that are harmful.

"Second: A mechanism in the neurones gives results in the behavior of the animal as a whole that seem beyond mechanism. By their unmodifiable abandonment of certain specific conditions and retention of others, the animal as a whole can modify its behavior. Their one rule of conduct causes in him a countless complexity of habits. The learning of an animal is an instinct of its neurones."

Of course the assumption that the neurones react so as to make themselves more permeable to stimuli that are beneficial, and to make themselves less permeable to stimuli that are injurious has no direct evidence in its support. Its value consists in its serviceableness as an explanation of learning. But notwithstanding the fact that reactions on the part of cells are very frequently teleological the hypothesis is, I believe, not in accord with what is known of the physiology of the nervous system. So far as we know, nervous impulses are the same in character everywhere. We should expect that up to a certain degree of intensity, like functional stimulation in general, nervous impulses would enhance the life processes of the neurones. Only when overstimulated would we expect that there would be any deleterious or annoying effects which are supposed to result in the reduction of the permeability of the synapse. Thorndike's doctrine then naturally leads to the position that the vitally good and pleasant stimulations are those of optimal or sub-optimal intensity, while stimulations of greater intensity would produce effects which are unpleasant and deleterious, at least at the time. Are the facts such as the theory would lead us to expect?

Stimulation of pain nerves produces sensations which are generally disagreeable in all degrees of intensity which can be appreciated. Shall we say then that all stimulation of the neurones involved in responses to pain giving stimuli are injurious to the neurones involved? If so, practically all functional stimulation of these neurones would be deleterious to them. On the other hand, certain sensory systems may be stimulated strongly for a long time without producing results that are unpleasant. It is far from proven that the sensations aroused by stimulating the nerves of touch, heat, and certain of the nerves of taste and smell are ever disagreeable, however strongly the end organs are stimulated. It is probable that most of the unpleasant results alleged to follow from overstimulating a particular sense organ arise from the fact that pain nerves become involved when the stimulating agent is sufficiently strong. This is very probable in the case of heat; and there is more or less evidence for the same conclusion in regard to very intense visual and auditory stimuli, although it can not be regarded as entirely established. Even were it proven that overstimulation of any sense organ produces unpleasant effects (and avoiding reactions as a secondary result), the unpleasantness may be due not so much to the injury to the overstimulated neurones as to the breaking over of the stronger neural current into new channels.

Certain tastes and smells are disagreeable even when they can barely be perceived at all, while others are welcome at almost any degree of intensity. It is very improbable that the disagreeable quality of the former is due to the supra-optimal stimulation of certain associated neurones. It is not so much the intensity of the effect produced by the stimulus that gives rise to disagreeable results and inhibitory effects as the channels through which the stimuli enter the nervous system. Were Thorndike's theory correct, we should expect to find comparatively mild stimulations producing, quite generally, pleasurable feelings, and strong stimuli producing disagreeable feelings, and, directly or indirectly, avoiding reactions. On the contrary, we find the organism provided with sets of reflex arcs, each of which tends to be set into operation by its own kind of stimulating agent, and producing feelings of much the same quality, however their intensity may vary.

Another consequence of Thorndike's theory is that reactions to disagreeable stimuli should become reduced the more often they occur. If a receptor is connected with neurones A, B, C, and D involved in a reflex response to a stimulus that produces disagreeable effects and an avoiding reaction, then as the neurones are, *ex hypothesi,* injuriously affected, the intimacy of their synapses would be weakened and the course of the impulse through the system more or less blocked. The disagreeable effects and the vigor of the avoiding response would therefore tend to wear away after successive repetitions. In general it cannot be said, I think, that this occurs. Castor oil ought, after being taken a few times, to become much less unpleasant, but I very much doubt if this is a common experience. People suffer pain from a particular region for years with little or no diminution of intensity, and there are some things which up to a certain point may become more disagreeable, instead of less so, the more often they are experienced. Sometimes, it is true, things which are at first disagreeable come to be tolerated in time with little discomfort, but this is probably because the incoming stimuli become connected with other neurones than the ones which gave the original motor expression. In other cases it may be due to quite different organic adjustments. It is doubtful if where the unpleasant stimuli continue to be responded to through the same channels, there is in general a weakening of the response or mitigation of its disagreeable quality. According to the theory, responses involving unpleasant effects should come to inhibit themselves. Such a result might shield the neurones from further injurious stimulation, but it would hardly be conducive to the welfare of the organism in general, since it should keep on reacting so as to avoid sources of injury. That there is any general tendency for unpleasant responses to become reduced in vigor, apart from the purely temporary effects of fatigue common to all responses, is very questionable.

On the other hand, there is probably no general tendency for pleasant responses to become performed with greater vigor or to be accompanied by heightened satisfaction. Learning to like certain articles of food as well as coming to dislike others is probably a matter of secondary association. Addiction to alcoholic drinks and other so-called habit-forming drugs is a phenomenon rather exceptional in character, the explanation of which need not concern us at present. Doubtless secondary associations are involved here also. It is probably not the initial pleasure which these drugs arouse that impresses the habit of using them (the subcutaneous injection of morphine, for instance, is the reverse of pleasant), but some general physiological effect which is pretty closely associated with their injurious influence on the neurones. Under certain kinds of intoxication a person may experience feelings of pleasure that go along with cerebral conditions which are decidedly unwholesome.

Ordinarily, pleasant tastes and smells retain very nearly their original algedonic quality. We may become more apt to seek a particular taste that we have had before, but this in no way goes to show that the original response set up by the pleasant substance takes place more easily or is attended with greater pleasure. Pleasures often wear away, and things once agreeable may come to pall upon us. There is little evidence that pleasure-giving stimuli in general tend to reinforce themselves, and where reinforcement occurs it is probably due to secondary associations with other reflex arcs.

The effects of agreeable and disagreeable states upon subsequent reactions to the stimuli immediately producing them are much the same. Considered as single responses both may be fatigued by repetition and influenced similarly by general bodily conditions. The notable thing about unpleasant responses is that they exercise their inhibitory influence on other reflex systems. It is chiefly in their influence on other associated reflex arcs that the different effects of agreeable and disagreeable stimuli become manifest. The nasty caterpillar in the mouth of a chick may not become less disagreeable when picked up on subsequent occasions, nor the edible worm may not give a more intense thrill of satisfaction, but the experience with the nasty caterpillar tends to check the pecking reflex, while the seizure of the edible caterpillar tends to reinforce it. Satisfying and annoying states do not affect the reactions by which these feelings are immediately aroused, but other reactions performed in close temporal relation to them.

The various theories put forward to explain the learning process as an effect of the physiological correlates of agreeable and disagreeable states are all open, I believe, to serious objection. Aside from the fact that no theory as to what these physiological correlates are is on a firm basis there is no one standpoint that gives a consistent interpretation of the process of learning. It is not evident that the correlates of all the varied states that are annoying have any general physiological characteristic which distinguishes them from the correlates of states which are pleasurable. And even if they have, it does not follow that these correlates are particularly concerned with the mechanism of association.

The view of learning sketched in the preceding chapter has at least the merit of avoiding any assumptions in regard to the physiological concomitants of agreeable and disagreeable mental states. The attempt was made to show that, given an endowment of instinct plus the ability to form associations, an animal may acquire modes of behavior which adapt it to new conditions of life. A response which results in setting into action a strong instinctive proclivity is reinforced or inhibited, as the case may be, according to its congruity or incongruity with the proclivity thus aroused. Ordinarily a response A that is closely followed by an instinctive reaction B involving the liberation of a considerable amount of nervous energy is reinforced, probably as a result of the influence of this energy on the nervous connections simultaneously excited by the response A. If, however, the associated reaction B is opposed to A, as when an outreaching action is followed by a withdrawing response, the influence of B tends to inhibit the first response A. In both cases, A and B tend to become associated, but the different secondary reactions have different effects on the primary response with which they have become joined.

Thorndike [1] has raised several objections to the view here discussed, but none of them, I believe, are fatal or even serious. "A secondary response R_2 may bind R_1 to S_1 [the primary response to the initial stimulus], even though it is incongruous with it, and disjoin R_1 from S_1 though it is congruous with R_1. Thus a cat in a box, the door of which is opened, permitting escape and eating *whenever the cat scratches herself,* will soon come to scratch herself as soon as put in the box, though there is no congruity between escape through a door and scratching." This objection is based on a misconception of the sense in which the word congruity was used in the statement of the theory criticized. Viewed as two external acts of the cat's body, there

[1] "Educational Psychology," I, 189, 1913.

is no apparent congruity between scratching and getting out and being fed. But when these acts have been performed a number of times in close sequence we cannot assume that they will not form a congruous association. The investigations of Pawlow and his co-workers have gone far to show that almost any two acts performed at nearly the same time may become associated. The salivary reflex of a dog may be set up through having become associated with sights, sounds, stimulation of the legs, or even the application of a painful electric stimulus. How the second act influences the first after the association has been formed is the important consideration, and we need not be surprised to find that certain responses are reinforced by acts of very diverse kinds.

"Again," says Thorndike, "if a cat is put into a box, X, with two alleys opening to the North from it, A and B, and if whenever it advances two feet into alley A it is hit from behind with a club and so runs on out of the North end of A, whereas, if it advances two feet into alley B, it is given a piece of meat and hit gently from in front, the cat will, when put into X, be less likely to advance into A and more likely to advance into B. Yet the response of advancing into A produced the congruous secondary response of advancing further in the same direction, whereas the response of advancing into B produced the incongruous retreat into X."

I think the experiment, however, is capable of a different interpretation. When the cat advances into alley A, gets a blow from behind and gives the avoiding reaction, she naturally comes to associate this avoiding reaction with the sight of that particular alley. This on a subsequent occasion would cause the cat to give the avoiding reaction upon the sight of A, and consequently prevent her from entering the scene of her former mishap. When the cat enters alley B, is given a piece of meat, and hit gently from in front and driven back, she is forced, it is true, to make, in one sense, an incongruous response, although she is not prevented thereby from entering B a second time. Thorndike does not consider the essential element of the situation according to the theory criticized as well as according to his own view,—namely, the reaction to the meat. Without this, the act of driving the cat out of the alley would probably have inhibited her further entrance. The association formed between entering the alley and eating the meat makes the entrance to the alley, as it were, a part of the meat-eating reaction, and the first response is repeated through having been coupled with the discharge of this strong instinctive propensity.

Those acts which elicit an animal's natural instinctive reactions are particularly prone to become associated with the latter, owing to the greater discharge of nervous energy which these instinctive reactions involve. The acts which are stamped in are those which are consistent with the performance of an instinctive activity which they have been the means of setting into operation. Where an instinct is very readily discharged, as in the case of the food-taking instinct of a hungry animal, acts which occasion this discharge tend to become quickly and firmly associated.

We may be justified in saying that certain instincts, such as that of devouring food, have a quite general tendency to reinforce acts which bring stimuli that form the occasion of their discharge. On the other hand, injurious stimuli may tend to inhibit quite generally other activities with which they have been associated. Animals are supplied with an elaborate equipment of avoiding reactions as a part of their congenital make-up, and as a result of the associations formed through experience they come to shun the things by which these avoiding reactions have been aroused. There is nothing *a priori* improbable in the assumption that animals may be congenitally endowed with connections in the central nervous system which would enable them to link up their various trial movements in ways which, on the whole, are serviceable. That such connections should exist is no more improbable than the occurrence of any other form of adaptive organization.

Profiting by experience in an animal of a primitive type of intelligence we may conceive, then, to take place as follows: The creature is endowed with the capacity for responding to beneficial stimuli by aggressive, outreaching movements, and to injurious stimuli by movements of withdrawal, retreat and avoidance. All these are matters of pure instinct. Given the power of forming associations between responses, the animal acquires new habits of action by repeating those responses which arouse instinctive acts of a congruous kind, and by discontinuing those responses which arouse instinctive acts of an incongruous kind. Modifications of behavior brought about in this way would, in general, effect a closer and more adequate adjustment of the organism to the stimuli that act upon it. The associations formed would be in the direction of refining the creature's instincts and adapting them to varied conditions of life. Intelligence so developed would be quite generally subservient to instinct, as in fact we find it to be, especially in its more rudimentary stages of development. The new things an animal learns to do are done because they have been assimilated to its instinctive activities.

The interpretation of learning which we have been considering ascribes an important rôle to reinforcement and inhibition. The essential nature of these processes, despite much investigation and speculation on the part of physiologists, still remains an enigma. If we thoroughly understood their nature and knew something more of the changes (whether in the synapses or elsewhere) by which associations are established, we should doubtless be able to penetrate more deeply into the mechanism of intelligent behavior. I would not be understood as claiming that the present account of the learning process is entirely adequate. There are too many little known elements in the process to warrant anything more than a tentative adoption of any one standpoint. But the view defended does not postulate the existence of any physiological processes beyond those known to be commonly manifested in the physiology of the nervous system. Nothing is assumed in regard to the physiological correlates of pleasure and pain, the teleological behavior of the neurones, or the nature of the changes on which associative memory depends. It is of importance, I believe, to determine how far we can explain intelligent behavior without multiplying entities by calling other factors to our aid. At present it is far from clear that it is necessary to make such an appeal.

VIII

THE IMPLICATIONS OF TRIAL AND ERROR

THE concept of trial and error is one that has played a prominent rôle in modern writings on comparatively psychology, and especially those which concern themselves with the problem of how behavior comes to be adaptively modified. The activities of animals must obviously be so shaped as to preserve the life of the individual or its race. To a certain extent successful acts may be hit upon by sheer accident, but for the most part the purposive behavior of an animal is due to its congenital make-up. According to the reflex theory of instinct, which commands a wide following at the present time, instinctive activities are fatally determined by structural mechanisms which are set going either by external or internal stimulations. In either case instinct, even in its most wonderful and complex manifestations, is, in essence, nothing but response to stimulus. And if we ask for an explanation of the teleological character of the responses we are referred to "inherited organization" for an answer. As the machine is constructed, so will it work.

Whatever the merits or demerits of the reflex theory of instinct, it is evident that many kinds of adaptive behavior occur in which the stimulus is responded to, not by a direct, appropriate act, but by varied movements which apparently have little relation to the source or nature of the stimulating agent. This is well illustrated by the behavior of the protozoan Paramœcium which has been so exhaustively studied by Jennings. Paramœcium, as it swims through the water, rotates about its long axis and describes more or less of a spiral path. When it encounters an object or receives a sudden stimulus of any sort it reverses the beat of its cilia, swims backward, turns to the aboral side and then continues on its way. It matters little on which side Paramœcium is stimulated; its reaction, which Jennings has called the "motor reflex," is practically the same. Sometimes the motor reflex brings the animal into closer contact with the stimulating agent. If so, the reaction is repeated, and continued so long as the animal is stimulated by the unfavorable conditions.

Paramœcia, like many other simple organisms, form aggregations in regions of dilute acids. They are not drawn to these chemicals from a distance, but if a Paramœcium happens to swim into the area of dilute acid it passes through to the boundary between the acid and the surrounding water where it gives the motor reflex and swims in another direction. If it again encounters the boundary it gives the motor reflex and swims away, so it is practically caught in a sort of trap. Other Paramœcia happening to enter the area are similarly caught, so that an aggregation of individuals is gradually formed. There is no orientation of the Paramœcia to the diffusing chemical. The acid does not attract the animals in any sense. The infusorians simply give the motor reflex when they swim from acid to water, and as a consequence of this simple reaction a collection of individual results.

Jennings has shown that Paramœcium responds by the motor reflex to nearly all kinds of stimuli. Practically its whole behavior is based on this trial and error method. The organism does not directly avoid injurious stimuli. The motor reflex may or may not relieve it from the stimulating agent. But it keeps on repeating the reaction until in time it chances to be brought away from the injurious stimulation. When favorable conditions occur, its behavior continues unchanged. The Paramœcium's philosophy of life is very simple. It consists in merely following the Pauline injunction: "Prove all things; hold fast that which is good."

The same general scheme of reaction Jennings found to be very widespread among the lower organisms. Although the reactions of the organisms may be simple and stereotyped, this scheme of response gives to the behavior of these forms a plasticity and adaptiveness that keep them away from injurious stimulations and in conditions favorable for their existence. Where there is "error," the organism tries again, and keeps on doing so until it attains ultimate success.

"Error" generally means any act prejudicial to organic welfare. The lower organisms are like ourselves in avoiding things which are injurious and in remaining under beneficial conditions, whether or not they are influenced thereto by similar psychic states. Jennings feels "compelled to postulate throughout the series certain physiological states to account for the negative reactions under error, and the positive reactions under success," but the search for such states, as I have elsewhere attempted to show, is probably a vain quest.

In behavior of the trial and error type, success is attained, not by a direct adaptive reaction, but by checking or reversing all reactions except the right one. The final outcome of the varied movements is adaptation. The method is roundabout and expensive, but it is better than nothing. It is Nature's way of blundering into success.

The capacity to gain anything through the method of trial and error presupposes that an animal's reactions to beneficial stimuli are different from its reactions to injurious ones. There is, as I hope to make clear, no way of acquiring this capacity unless there is a congenital basis of adaptive response to start with. We are led to the conclusion that the adaptive character of the indirect adjustments effected through the method of trial and error is, like the adaptiveness of direct instinctive responses, the outcome of inherited organization.

This conclusion applies to intelligent behavior as well as to the more primitive forms of indirect adjustment. That the burnt child dreads the fire depends upon the fact that there is an innate reflex tendency to jerk back the hand when it comes in contact with a hot object. We have therefore a bit of primary adaptive responsiveness to start with. Experience links up the sight of the object with this primary reaction. Association *per se* has nothing teleological about it, but it is a means of effecting further adjustments, or rather perhaps of applying to new conditions the adaptive responses already present. If an organism were constituted so as to respond to all stimulations in a perfectly hit or miss fashion, without any reference to its own welfare, it is not likely, even if the creature had the power of forming associations, that it would be able to profit by experience. Suppose, for instance, it should react to the sight of an object by an act of seizure. Suppose that contact with the object, which we will suppose in this case to be food, should evoke an avoiding reaction instead of the usual purposive movements. The sight of the object becoming associated with the avoiding reaction would cause an inhibition of the first response by calling into play an antagonistic reaction. If food were responded to by an avoiding reaction, the associations acquired by experience, while they might modify behavior, would not help the animal out of its unfortunate situation. Merely associating experiences is of no particular value. There must be some principle of selective association if experience is to be turned to any account, and this principle is supplied by the animal's stock of congenitally adaptive reactions. What makes intelligence of any value to its possessor is its ingredient of primary purposive responsiveness. Without this ingredient, which is the real controlling hand in an animal's life, behavior would be a mere chaos of misdirected activity. It is really instinct that makes intelligence useful.

If the adaptiveness of intelligence rests upon the adaptiveness of instincts and reflexes, and if the latter is determined by inherited organization, we must look to the forces that have moulded organization, i. e., the factors of evolution, for the primary source of adaptiveness in behavior. Aside from the very doubtful rôle of the Lamarckian factor, we have at present no way of explaining how purposive organization can evolve, except through the operation of natural selection. Given variation (which may be quite fortuitous), struggle for existence, and the survival of the best endowed, adaptive organization will be the outcome. Natural selection is itself a sort of trial and error process, a method of getting a successful product out of variability which, so far as adaptation is concerned, there is no reason to believe is other than of a random, hit or miss character. Whether the principle of selection will account, directly or indirectly, for whatever there is of purposiveness in organization and behavior is of course an open question. But there is no other factor which is certainly operative in shaping descent along adaptive lines, and as entities are not to be multiplied beyond necessity, it is, I believe, justifiable to adhere to the theory of selection until its inadequacy is clearly established.

The position to which we are led is that the securing of any advantage through the method of trial and error presupposes congenital modes of response which are adapted to secure the welfare of the individual. The method is not the primary source of adaptive reactions so far as the individual is concerned. It cannot be the primary source of adaptive behavior in the evolution of the race. A method of blundering into success instead of attaining it directly, it would be of no service unless the organism were capable of turning to profit its fortunate trial movement. In order to do this the organism must be provided for the situation by its inherited endowment.

Certain writers on genetic psychology have attempted to explain the beginnings of adaptive reactions on the basis of individual experience alone. Given an organism which just responded to stimuli in a perfectly random manner, they attempt to show how the environment would discipline it into acting in accordance with its own welfare. Aside from those functions which Jensen has included under the primary purposive attributes of life (primäre Zweckmässigkeit), and which must be presupposed if an organism is to be an organism at all, we naturally suppose that during the early periods of evolution there has been a gradual substitution of adaptive for non-adaptive modes of behavior. If the new adaptations arise in and through experience they must be transmitted by inheritance if they accumulate to the advantage of the race. But aside from the difficulties which beset the theory that such acquisitions are inherited, there is involved the further difficulty of understanding how, in the beginning, adaptations could have been acquired at all. To this the Lamarckian might of course reply that it is a fact that adaptations do arise through individual experience, however we may account for them, and that it is not especially incumbent upon him, *qua* Lamarckian, to explain their origin. There is no gainsaying the pertinency of the Lamarckian's answer as regards the origin of many purposive forms of behavior. If, however, it can be shown that the ability to acquire special adaptations rests upon innate modes of reacting to stimuli, and that in so far as acquired characters are adaptive, their origin presupposes the existence of congenital adaptive reactions, the Lamarckian can no longer dodge the responsibility of explaining how these congenital reactions came to be of service to the organism. Unless the characters acquired by experience were useful their accumulation through inheritance would obviously be of no value. Lamarckism practically rests upon the assumption that an organism's natural modes of response are teleological. But it gives no account of how they came to be so.

Can an organism that responds totally without regard to its own welfare, if such an organism can be imagined, ever be hammered into an adaptively reacting mechanism through the influence of the environment? Spencer's and Bain's theories of the origin of adaptive movements practically assume that it can. Both Spencer's and Bain's theories assume that adaptation is brought about by a process of selection from among the various random activities performed by the organism. It is the accidentally adaptive movement that comes to be repeated. Both theories assume that the adaptive movement is repeated because it brings pleasure to the organism. Hence there must be a correlation not only between pleasure and welfare, but between pleasure and the tendency to repeat an action by which pleasure is secured. To the question as to how pleasure came to be associated with organic well being, Spencer falls back upon natural selection for an answer. Organisms in which the pleasurable coincided with the organically beneficial were preserved, while the others perished, so there gradually came to be established the general relationship between the pleasant and the beneficial which we commonly find. So far as I know, no other plausible account of this relationship has been offered. The Lamarckian explanation of the origin of adaptive movements which Spencer himself adopts has to work with relationships which, as Spencer himself admits, have been established by natural selection. It is the congenital make-up of the organism that determines which of its various random movements comes to be selected. In the absence of the proper hereditary endowment the organism might make random movements all its life without securing any desirable result. No one has yet succeeded in showing how a bit of undisciplined protoplasm is able to acquire any form of adaptive behavior.

We are brought to the conclusion that the ability to profit by experience, both in its higher manifestations as intelligence and in the simpler forms of organic adaptation, involves an organism moulded into at least partial conformity with its environment. The activities that are described as "trials" afford increased opportunities for adjustment, but the ability to take advantage of successful trials rests upon the basis of congenital endowment. It is inheritance that affords the means by which inheritance is improved.

REFERENCES

BAIN, A. The senses and the intellect. 3d ed., 1894.

BALDWIN, J. M. Mental development. Methods and processes. 2nd ed. N. Y., 1903.

Jennings, H. S. The behavior of lower organisms. N. Y., 1906.

Jensen, P. Organische Zweckmässigkeit. Jena, 1907.

Spencer, H. Principles of Psychology. N. Y., 1892.

Torrey, H. B. The method of trial and the tropism hypothesis. Science, N. S., 26, 313, 1907.

IX

BEHAVIOR AND FORM

THE idea has been recently emphasized that in many cases the structure of an organism is, to a considerable extent, the effect of its behavior. We have, of course, long been familiar with the fact of functionally produced modifications, but it is only of late that behavior has been brought forward as a factor of importance in development, regeneration and other modes of form regulation. If the way in which an organism acts is determined by its structure, it may also be said that its structure is to a certain degree determined by the way in which it acts.

The experiments of Child on the regeneration of planarians, nemerteans, and other forms have led him to the view that one very important element determining the way in which a part differentiates is the kind of movements it is called upon to perform during the period of its formation. A posterior cut end of a planarian, for instance, develops a tail because owing to the movements of the animal, the regenerating tissue is subjected to the same impacts and tensions to which the tail end of the entire animal is normally subjected. These activities impressed upon the regenerating part are regarded as the directive agents in the process of differentiation, and if the animal were to act in a very different manner quite different formative processes would result.

Child found that in pieces of Leptoplana which were caused to creep in a circular course owing to unilateral injury of the anterior end the new tail that was formed, instead of growing out posteriorly, developed in an oblique position in accordance with the altered activity. "The regenerating part grows in the direction of the principal tension, even though this forms an angle of 90° with the principal direction of growth." In speaking of the ordinary activities of Leptoplana, Child says: "It can scarcely be doubted that these movements play a part in shaping the regions in which they occur. A comparison between frequency, amplitude, and force of the undulating movements and the degree of lateral development in the regions in which they occur is most striking. According to the usual point of view, this correlation between structure and function is merely one of the many remarkable cases of adaptation, but in my opinion it is, at least in part, the direct result of function in the individual. . . .

"As regards the manner in which the movement may affect the tissues it is not difficult to see that the movement of these parts to and fro through the water must subject them to tension in the lateral direction. This must affect in greater or less degree the distribution and arrangement of the plastic tissues composing the parts. A very simple physical experiment serves to illustrate this point. A cylindrical or square stick of sealing wax moved to and fro in water sufficiently warm to soften it will undergo flattening in a plane at right angles to the direction of movement. The change in form is more strikingly shown if a rigid axis is present; a mass of wax molded in cylindrical form about a stiff wire will become in a few minutes a thin flat plate decreasing in thickness towards the edges and with a rounded outline. The mechanical conditions resulting from the movement of the wax through the water are not widely different from those which the undulating margins of Leptoplana produce. If the wire axis of the wax be considered as the longitudinal axis the effect of movement through the water is lateral extension. In Leptoplana the undulating movement is confined chiefly to the lateral regions in the anterior third of the body and it follows that the conditions described are limited chiefly to these parts."

"There can be little doubt, in my opinion, that these mechanical conditions constitute a factor in the formation of the broad lateral regions in Leptoplana and more especially in other forms in which the undulating movements of these parts occur. In other words, the form is in some degree the result, not the cause, of the characteristic method of activity."

In experiments on Planaria Child has shown that the head and pharynx do not attain their normal shape and structure when movement is largely inhibited by anæsthetics, but he does not conclude that movement is the only factor involved. Regeneration and all other modes of the regulation of organic form he regards as the outcome of functional regulation. Movement plays a certain rôle in shaping the outline of some organisms, especially those with physically plastic tissues, but "it is merely one of a great variety of functional factors."

While studying the regeneration of the infusorian Loxophyllum I found that I was dealing with an organism in which regeneration and behavior are apparently closely connected. Loxophyllum is a flattened infusorian that moves by gliding on the bottom on its right side. It confines its activities usually to a small area for a considerable time; first it glides forward a short distance, then reverses its cilia and swims backwards, turns toward the oral side and then swims forward again in a new direction. As the animal swims forward the body is elongated, but as it goes backward the body is invariably shortened and widened, thus showing a constant association between the direction of the beat of the cilia and the contraction of the myonemes. In the changes in the form of the body it is the contraction and extension of the oral side that play the most important part, and it is along the oral side that the myonemes are especially abundant and of large size. In going forward the body bends orally and frequently undulates about in a very variable manner. The backward and forward movements of Loxophyllum may be performed in much the same way for a long period apparently without any external stimulation. The organism is capable of many kinds of behavior under different conditions, but its usual activities are all that concern us in the present connection.

As has been found in other infusorians, the behavior of pieces into which the organism is cut is closely similar to that of the entire individual. The pieces of this species regenerate so rapidly as a rule that one can actually watch the process going on. An excellent opportunity is thus afforded for studying whatever connection there may be between the activities of the piece and the changes of form that occur in it.

In the regenerative changes of the posterior half of the body, for instance, we find that apparently as a consequence of the elongations and contractions that accompany the forward and backward movements, the general form elongates and becomes more narrow. The cut end is partially closed in by the drawing together of the two margins, the oral side extending over rather more than the aboral (Fig. 1). In the movements of the animal it may readily be seen that the oral side is pushed ahead as the animal swims forward as if it were making active efforts to stretch itself out. Both margins, however, take part in this active extension, but the oral side is the more active and soon it may be seen to push around the anterior end of the body, and its myonemes and cilia are thus brought into the characteristic curvature which is found at the anterior end of the entire organism.

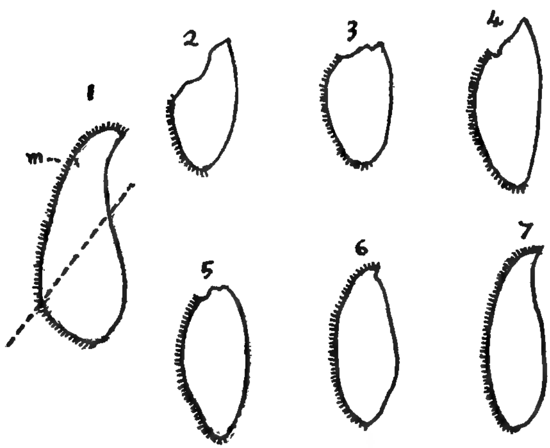


Fig. 1.—Regeneration of posterior piece of Loxophyllum. The dotted line indicates the direction of the cut. The figures 2, 3, 4, etc., representing the successive stages of the process, show the gradual stretching of the ciliated margin. m, mouth.

If the cut is made obliquely (Fig. 2) so as to limit considerably the extent of the oral side, the same method of regeneration is followed, the oral side is gradually stretched out so as to form the oral side and anterior end of the new individual.

In the process of regeneration here followed the final form of the organism is reached by the simplest and most direct means,—there is a minimal amount of formation of new structures. The cut end does not differentiate any new organs, but the old differentiated parts are stretched out to form the structures of the new individual. It may readily be seen that the activities of the organism in

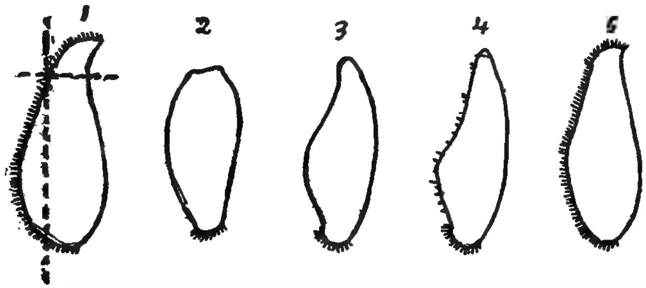


FIG. 2.—Regeneration of Loxophyllum after being cut, as shown by the two dotted lines. The small part of the ciliated margin that remains is stretched but a short distance, while new cilia are formed along the new oral margin.

extending, contracting the body and in constantly pushing the oral side farther ahead than the aboral, tend to mould the piece into the normal form of the species. In other words it might be said that the organism pulls itself into shape. The piece gets pulled into the form of the entire animal because it behaves essentially like the entire animal.

So far the results seem to support the view that form is the result of activity, at least to a considerable degree. But instructive developments are yielded by further experiments. By making a cut so as to remove all the oral margin with its differentiated structures we compel the organism to follow a quite different method of regeneration (Fig. 3). At first, owing to the absence of the more contractile and extensile elements of the oral

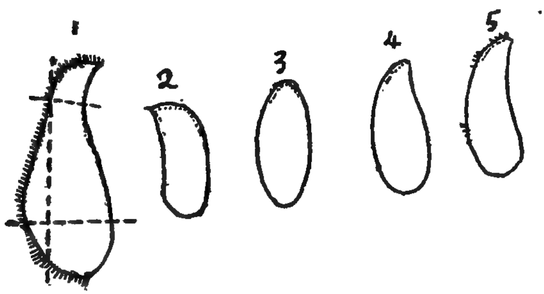


Fig. 3.—Regeneration of Loxophyllum after removal of entire oral margin.

side, the aboral margin in the movements of the animal are pushed farther ahead than the oral. The organism elongates and becomes pushed over toward the oral side. Later, however, the oral side becomes thinned out and more transparent; cilia make their appearance in scattered groups, new trichocysts are developed, and contractile threads appear in the thinned out region. After these various structures are developed the oral side begins to extend and contract more than the aboral. Then it becomes pushed ahead more and more, and finally is carried around the anterior end of the body as in the normal animal.

In this experiment the animal is forced to follow a method of regeneration very different from that pursued in the experiments previously described. The old differentiated parts are not stretched out to form the new ones, but the structures of the oral side of the new individual are formed *de novo*. It is an interesting fact that the time required for regeneration in the first case is short, the process being completed in a little over an hour, while in the latter case it was not completed until about fifteen hours. In the latter experiment the characteristic behavior of the oral side had to wait upon the differentiation of the oral region of the body. Where regeneration is apparently produced largely by the organism pulling itself into shape through its characteristic movements behavior seemed to lead the way in moulding the normal form. In other experiments the characteristic movements had to wait until the finer differentiations of the organism were developed by other factors; then behavior stepped in to help mould the already differentiated organism into its normal outline.

I think that the foregoing experiments (and I have described only a small part of the number that were made) indicate that the more fundamental factors in the regeneration of this organism are not so much its gross activities as various internal factors which we need not here attempt to specify. At the same time the behavior of the infusorian is a link in the chain of causes by which the final form is brought about, but it is concerned more in determining the general shape of the body than the finer details of its internal structure.

What is true in this case has, I believe, a rather general application. The gross general behavior of an animal plays, I believe, a subordinate though at times an important rôle in the determination of organic form. But when we turn our attention to the internal processes which are responsible for the finer details of organization may we not again encounter problems of behavior? May not the differentiation of these parts be, to a considerable degree at least, the result of the behavior of their component elements? The study of differentiation in higher organisms where it is possible to follow the activities of the various cells which make up the body makes it evident that such is the case. The rôle of this factor will be considered in the chapter on The Behavior of Cells.

REFERENCES

Child, C. M. (1) Studies on regulation. IV. Some experimental modifications of form regulation in Leptoplana. Jour. Exp. Zool. 1, 95, 1904. (2) The regulatory change of shape in Planaria dorotocephala. Biol. Bull. 16, 277, 1909. (3)

Analysis of form regulation with the aid of anæsthetics. l. c. 16, 277, 1909.

HOLMES, S. J. Behavior of Loxophyllum and its relation to regeneration. Jour. Exp. Zool. 4, 399, 1907.

X

THE BEHAVIOR OF CELLS

SINCE the epoch-making promulgation of the cell theory by Schleiden and Schwann biologists have commonly looked upon the component cells of the body more or less in the light of little organisms, each with its own individuality, each carrying on the business of its life to a certain degree independently of its fellows. Haeckel speaks of a cell soul which he regards as a quasi-discrete bit of psychic life. Binet in his *Psychic Life of Micro-organisms* writes of the various psychic faculties manifested by the white blood corpuscles and other cells of our bodies. And Lloyd Morgan in his book on *Animal Behavior* devotes a section to the behavior of cells and shows how various formative processes are to a considerable extent the outcome of coordinated cell activities.

The study of cell behavior has been greatly stimulated by the development of a branch of biological investigation, variously known as developmental mechanics, physiology of development, etc., which has for its aim the analysis of embryonic development, regeneration, and other formative activities, —in a word, all those processes which lead to the production and maintenance of the normal form of the organism. The science of developmental mechanics is of very recent growth. Its already numerous devotees endeavor to gain a deeper insight into the nature of development than it is possible to obtain by the older methods of descriptive embryology. However full and exact our knowledge may be regarding the cleavage of the egg, the formation of the germ layers, and the differentiation of organs; however thoroughly we may come to know the sequence of events which lead from the egg cell to the adult animal, such knowledge does not necessarily reveal the threads of causal connection that govern the course of development. The development of any organism is a wonderfully complex process. We may describe what goes on with the greatest fidelity to every detail, but the causal relations are so involved that we can seldom discover them without special methods of analysis. The science of developmental mechanics set itself the task not merely of describing what takes place but of explaining why it takes place. Description it regards as subsidiary to explanation. Having for its aim the search for causes, it naturally adopts experimentation as its chief method. Developing eggs are shaken apart, subjected to heat and cold, to chemicals and a great variety of other external agents; particular parts of the embryo are removed, displaced, or replaced by other parts, and all sorts of modifications of development are induced in order to discover something of the relations of dependence subsisting between the various activities which lead to the formation of the embryo.

When one watches the early development of the egg of a mollusk or annelid worm, follows the regular and almost mathematically precise way in which cell division occurs, and the method by which the cells become arranged in a perfectly regular pattern, then observes the infoldings and overgrowth that lead to the gastrula stage, and the differentiation of particular cells to form the organs of the embryo, he cannot escape a feeling of wonder that a bit of simple material, such as the undivided egg appears to be, contains such powers of elaborate and well-ordered construction. A marvellous builder this bit of egg substance! It is comparatively easy to make a sort of rough catalogue of the methods it employs. Development may be said to be an affair of cell division, cell growth, cell differentiation, changes in the form of cells, changes in their position, etc.; but this cataloguing of processes is a mere preliminary to the business of further analysis. In order to build up an embryo, cells must divide, they must in most cases grow, and they must get into the right relative position and differentiate, some in this way and some in that, so as to establish a harmoniously working mechanism. In most organisms formative processes involve a considerable amount of cell movement. Sometimes this is passive, as when cells are pushed or pulled by means of osmotic changes or growth processes occurring in other parts. But it is coming to be recognized more and more that many of the processes of embryonic development are the result of active cell movement. Many cells in early development have a considerable power of locomotion, and, like the soldiers of a well-disciplined army, they move into their appointed places at the proper time. To gain an insight into this feature of their development, to understand why it is that these cells act as they do, we are naturally led to a study of cell behavior. To a considerable extent the form of our bodies is an expression of shall we say cell psychology? Or, at any rate, it is in part the expression of that kind of behavior which is embraced under comparative psychology when found among lower organisms.

A few years ago Wilhelm Roux, an investigator of especial prominence among the experimental embryologists, found that if the cells of the frog's egg are shaken apart during early stages of segmentation, and placed in water a short distance apart they would slowly approach one another until they came into contact. This peculiar behavior, which was later observed also by Rhumbler, was called by Roux Cytotropism. Whether it is a form of chemotaxis, or just how it is brought about is uncertain. Cells of the early cleavage stages also show a marked tendency to come into contact with one another as closely as possible. While they round up during division, during the resting stages the cells fit together so as to leave no spaces between them. This trait not only tends to keep the cells in a compact mass, but it has other important functions as we shall see later on.

The cells of the embryonic tissue called mesenchyme have long been noted for their powers of migration. These cells are usually irregular and changeable in outline, and are able to creep about much like an Amœba. Usually they form masses lying between other cell layers. Their origin is varied, and they frequently move to a considerable distance from their source. An excellent illustration of their behavior is afforded in the early development of the sea urchin. In the region of the hollow blastula which is being pushed in to form the primitive gastrula cavity there is given off into the interior of the embryo a number of amœboid cells. These wander away from their point of origin and take up positions on opposite sides of the archenteron, where they form two groups. Why do the mesenchyme cells take up their position in these particular places? Driesch found that by vigorously shaking the young embryos the mesenchyme cells became loosened and scattered about irregularly in the cleavage cavity. After the embryos had been left for some time, however, it was found that these mesenchyme cells were back again in their normal position as if they knew what was their appointed function and took up their station accordingly. We may conjecture that it was some chemotactic influence that drew these cells to certain regions of the embryo much as white blood corpuscles are attracted to substances produced by certain bacteria; or possibly it may have been some form of reaction to contact stimuli; but, anyway, the result is of interest in showing the rôle played by cell migration in establishing the structure of the embryo.

The mesenchyme cells of the embryo are the parents of most of the connective tissue cells of the adult organism. The latter have long been known to be more or less migratory under certain conditions, and the recent work on the cultivation of tissues outside the body has shown that they possess considerable power of amœboid movement. When a piece of tissue, especially from an embryo or young animal, is mounted in a hanging drop of blood plasma there soon appears around it a ring of more or less spindle-shaped cells radiating into the surrounding medium. These spindle-shaped cells are derived mostly from connective tissue, and the ring that is formed results chiefly from the outwandering of cells, although in some cases the growth and multiplication of cells undoubtedly contribute to its formation. The writer has often watched the movements of these cells under the microscope. The locomotion is essentially amœboid, and the cells show a pronounced thigmotaxis, or tendency to keep in contact with solid bodies.

The pigment cells of many animals are related to connective tissue cells both in origin and mode of behavior. In many crustaceans, fishes, amphibians and reptiles the pigment cells appear at times to be richly provided with branched processes, and at other times nearly all the pigment appears to be concentrated in a rounded mass. These changes often produce marked changes in the color of the animal. They are to a certain extent under the control of the nervous system, but they may also take place independently of nervous influence. The writer has succeeded in isolating pigment cells from

Fig. 4.—Successive changes in the form of an isolated pigment cell from a frog.

various amphibian larvæ and also from the adult frog and in keeping them alive in hanging drops of blood plasma where their various changes in form could be followed with the greatest readiness. The pigment cells were seen to undergo changes in form similar to their changes in the skin, putting out processes here, drawing them in there, and in some cases creeping along the cover glass for a considerable distance. These cells, like their relatives, the connective tissue cells, have a strong positive thigmotaxis. Loeb found that in the embryos of the fish Fundulus they tend to appear along the course of the blood vessels of the yolk sac, thereby producing a certain color pattern characteristic of the species, a result probably due to some tropism, either a chemotaxis toward oxygen, or a thigmotactic reaction to the walls of the blood vessels.

Both connective tissue cells and pigment cells when isolated tend to withdraw their processes under unfavorable conditions and assume a spherical form. Too high a temperature tends to cause this response, and the same reaction commonly results when the culture medium becomes contaminated by the accumulation of metabolic products. An Amœba under similar conditions behaves in essentially the same way.

As is well known, the cells of epithelial tissues are almost always arranged in definite layers one or more cells thick. Such tissues are found covering the entire surface of the body, and lining all the inner surface of the alimentary canal and its various appended organs; epithelium forms the inner lining of the body cavity, the blood vessels and lymphatics; in fact, in almost every situation in which a free surface occurs it is covered by a layer of this tissue. If for any reason a part becomes denuded of its coating of epithelium it is usually rapidly covered again by extensions of this tissue from contiguous areas. There have been various opinions as to just how this extension is brought about. Several investigators have concluded that it is mainly effected by the migration of epithelial cells, and the recent work of Leo Loeb, Oppel and Harrison tends strongly to confirm this view.

A particularly favorable method of studying the problem is presented by the cultivation of epithelial cells in some nutrient medium outside the body. The writer has employed this method in the study of the epithelium of larval and adult amphibians. It was found that a piece of epithelial tissue kept in a hang-

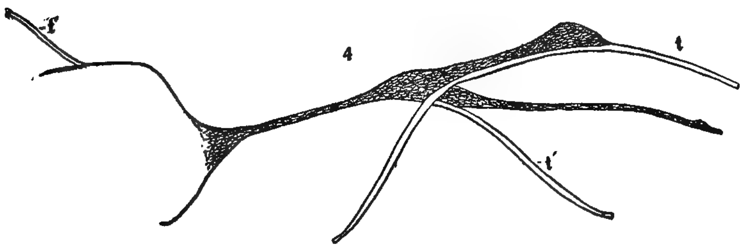
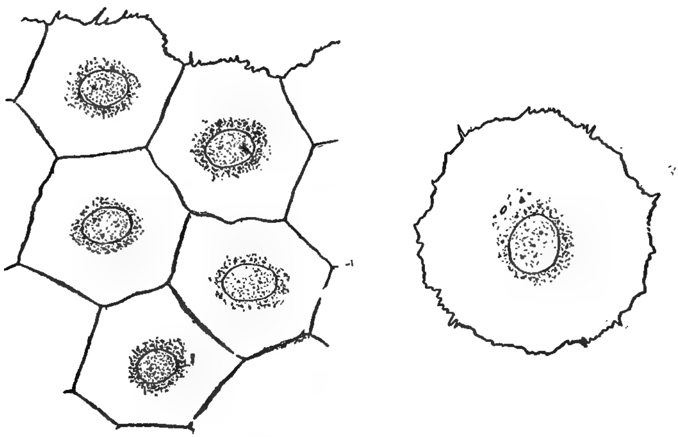


FIG. 5.—Strands of epithelial cells extending along and between fibers of cotton, tt and t′ t′. The dark part represents the outgrowth from a piece of a frog tadpole cultivated in lymph.

ing drop culture soon showed a fringe of flattened cells extending into the culture medium. In some cases the area of the extending tissue was over twenty times that of the implanted piece. Examining with a high power of the microscope the margin of the epithelial extension, numerous very fine processes or pseudopodia were seen extending in the direction of movement. These processes were seen to be in constant change. They are the active agents in causing the sheet of cells to be pulled out, for they are both adhesive and contractile. The effect of their activity is to cause epithelium to spread more and more widely, and in several preparations that were made, practically all of the available solid surface was covered by an investment of epithelium. If individual cells are isolated they frequently spread in every direction until they become flattened to an extreme thinness, and I have observed scattered individual cells flatten out until the adjacent cells

FIG. 6.—Successive stages in the advance of a strand of epithelial cells from a frog tadpole. This represents on a more enlarged scale the end of the strand lying between the two fibers of cotton t and t′ shown in Fig. 5. The dotted line indicates a fixed position.

met, forming a continuous membrane, scarcely distinguishable from certain epithelial membranes found in the body. The marked thigmotaxis of these cells leading them to spread over surfaces and to keep in close contact with one another is a very important factor in bringing about the layered arrangement characteristic of epithelial tissue, as well as in causing this tissue to form a coating over the exposed surfaces of nearly all organs of the body. Epithelial membranes usually form surfaces of secretion and absorption which separate regions of different osmotic pressure. It is essential to the performance of many important functions that these membranes be absolutely continuous with no apertures at any point. This continuity is insured through the traits of behavior we have mentioned.



A B

FIG. 7.—A secondary membrane formed by the approximation of originally isolated cells from the ectoderm of Hyla, such as shown in B. Very fine pseudopodia are shown in the free margins.

One very general and important feature of bodily organization therefore is traceable largely to certain peculiarities of the behavior of cells. In many animals the sex cells arrive at their final position only after considerable migration. In the sponges they are derived from amœboid cells and in hydroids they often migrate from one germ layer to another. In the eggs of many insects where they are differentiated very early in development they have been observed actually to pass outside the embryo for a time only to wander back again. Hegner has performed the experiment of removing these cells at the time they passed out of the egg and found that no sex cells developed in the resulting animal. In the embryos of several of the lower vertebrates Dr. B. M. Allen has found that the sex cells arise in the entoderm. Then they wander out along the rudiment of the mesentery and take up their final position at a considerable distance from their point of origin. As to what causes the movements of these cells and guides them in their course we can only offer but very tentative conjectures.

One of the most remarkable features of development is the way in which nerve fibers grow out from the central nervous system and push their way between various masses of cells to become connected with the proper end organs. The organism is permeated with a network of these fibers, spun out as fine as gossamer threads and connected with one another and with various parts of the organism in a very intricate way. In order to build up this elaborate and delicate system the nerve fibers as they grow out from the developing brain and spinal cord must take the right paths and connect particular groups of cells in the central nervous system with corresponding parts of the body. Should nerve fibers not find their proper termination all sorts of functional disturbances would result. What is it that guides the nerve fibers to their proper goal?

One widely accepted theory of the development of the nerve fiber is that it represents an outgrowth from the nerve cell. Harrison by cultivating in hanging drops of lymph small pieces of the nervous tissue from amphibian embryos has been able to observe the actual outgrowth of nerve fibers from the ganglion cells, and to study various stages in the process of outgrowth in living material. Harrison observed that the extreme tip of the outgrowing nerve fiber was often expanded and irregular in contour, and that it underwent amœboid changes as the fiber extended through the lymph. It is not improbable that this amœboid activity is the cause of the drawing out of the nerve fiber.[1] The factors, chemotaxis, thigmotaxis, or whatever they may be, which direct this amœboid activity may be responsible therefore for the distribution of the nerve fibers in the body and the establishment of the numerous connections that occur within the nervous system itself. The architecture of the nervous system, the great controlling element in behavior, is not improbably itself a product to a large extent of the peculiar behavior of its component cells.

[1] That the nerve fiber is actually drawn out in the way suggested has recently been shown by Mr. J. C. Johnson in his studies of the nerve cells of amphibian larvæ. Reference may be made to his paper on "The Cultivation of Tissue of Amphibians," published in the Univ. of Calif. Publ. Zool. Vol. 16, p. 55, 1915.

Among the most motile of the cells of the body are the leucocytes or white blood corpuscles. These cells are very much like Amœbæ in their appearance and their activities. They have the property of creeping about in the various spaces of the body and of passing through the delicate walls of the capillaries. Their power of engulfing bacteria and fragments of broken-down cells is well known. They act not only as the scavengers of the body, but by virtue of their power of destroying bacteria they defend the body against various disease germs that constantly invade it. Apparently they are drawn to centers of bacterial infection by a sort of chemotaxis. This is shown by an ingenious experiment by Massart in the following way: A tube of culture medium containing a culture of the bacterium *Staphylococcus pyogenes albus* was introduced into the abdominal cavity of a rabbit. After a time it was found that the leucocytes had wandered into the tube in large numbers. A similar tube filled with the same medium but containing no bacteria was also introduced, but it was not entered by the leucocytes. It is probable, therefore, that some substances produced by the bacteria caused the leucocytes to enter the tube.

The species of bacterium used in the experiment is one of the common forms that give rise to the production of pus. This substance which so frequently gathers in inflamed areas is produced mainly by degenerated leucocytes which have accumulated at the seat of injury. The aggregation of these wandering cells may actually be observed under the microscope in the transparent living mesentery of the frog. If a part of the mesentery is drawn out of the living animal and stretched over the stage of a microscope the blood may be observed streaming through the capillaries, and the individual corpuscles distinctly followed in their course. If a region near a capillary is pricked with a hot needle the white corpuscles may be seen to pause in their course as they arrive near the injured area and pass through the capillary wall. Here again it is probably some chemotactic proclivity that causes the leucocytes to congregate. Combined with the power of these cells to devour bacteria this chemotactic tendency enables the leucocytes to play the part of watchful protectors in checking infections and destroying products of decay.

Besides their rôle in maintaining the normal activities of the body the leucocytes often play an important part in development. In the formation of an organism the tearing down of previously established structures is often a necessary preliminary to further advance. The resorption of the tail of the tadpole is a process of involution in which the leucocytes play an essential rôle in destroying the fragments of the degenerating structure. The organs of the caterpillar are very largely destroyed in the quiescent pupa state in which the reorganization of the body occurs that results in the formation of such a very different creature as the butterfly. Here cells much like the leucocytes act as devouring cells or phagocytes which engulf the materials of the degenerating tissues.

Apparently the leucocytes are omnivorous in their appetite. One of my former students, Dr. Fasten, who has made a thorough study of the behavior of these cells, finds that they engulf even such substances as sulphur and chrome yellow, which would be rejected by an Amœba or almost any other free organism. This indiscriminate appetite would be fatal to a creature living a free life. Probably it is not particularly good for the leucocytes; but it must be remembered that the rôle of these cells is primarily altruistic. They work for the welfare of the body physiological. They are reproduced not so much from other leucocytes (although this process occurs) as by the division of cells in bone marrow and certain other organs of the body. They are meant for sacrifice after a life of service. And Nature has made them rather more than usually unmindful of their individual welfare.

However these cells do show many of the purposive reactions so commonly found in free organisms. Dr. Fasten by a delicate apparatus has succeeded in bringing the point of a very fine glass rod against one side of the cell. The leucocyte thus irritated put out pseudopodia opposite the point of the rod and crept away from the stimulus. The method of response was practically the same as that of an Amœba under the same conditions. Like Amœba also the leucocytes were found to be negative in their response to light, and when subjected to too high a degree of heat they withdrew their pseudopods and assumed a rounded form.

It would be of interest to ascertain how the various other moving cells react to different kinds of stimulation. I have tried the effect of localized mechanical stimulation, light, and heat on pigment cells, epithelial cells and cells from connective tissue, but found no reaction to light, no marked tendency to crawl away from injurious mechanical stimuli, but a general tendency to round up under too high a degree of temperature. The freely wandering tissue cells do not appear to possess that repertoire of adaptive responses which the leucocytes have in common with the Amœba. Probably fuller investigation will reveal more adaptive behavior in the cells of many forms. We know as yet next to nothing in regard to this field of inquiry, but it is one which promises to afford interesting results.

In that fascinating group of primitive organisms, the slime molds, formative processes stand in a more obvious relation to cell behavior than in the higher organisms. The coming together of individual cells, their union to form a creeping plasmodium like a gigantic Amœba, the transformation of this plasmodium into a definite form characteristic of a particular species,—all these processes are for the most part matters of the behavior of cells. If we can interpret development anywhere in terms of the tropisms and other responses of individual cells this peculiar group of organisms would seem to present unusually favorable opportunities for attacking the problem.

In a very interesting series of experiments Prof. H. V. Wilson has cut various sponges and hydroids into pieces, pressed the tissues through fine bolting cloth so as to reduce them practically to masses of isolated cells. It was found that these cells began to come together and form aggregations which subsequently differentiated into the form of the species from which the fragments were taken. Out of a hodge-podge of all sorts of cells one sees the gradual emergence of an organic body. The proponents of the conception of a cell state could scarcely hope for a better illustration of their point of view. It is as if a group of independent cells had said among themselves: "Behold, let us creep together and form an organism. If some of us do this, some that, and others something else we will all get along in peace and harmony and moreover much to our mutual advantage."

How a cell differentiates as well as what it does in the way of behavior depends largely on the relations in which it stands to other cells. The direction of differentiation which a cell follows may be looked upon as a response to environmental stimuli, just as the movements of a cell may be so regarded.

The energy evolved as a consequence of stimulation may be employed mainly in producing structural modifications of the cell substance, or it may be expended mainly in producing motor reactions. The response is usually purposive and social in either case.

Zur Strassen in a discussion of "Animal Behavior and Development" before the Seventh International Zoological Congress at Boston called attention to the social behavior of cells and the analogies between such behavior and the activities of social insects. The comparison is suggestive, but as Zur Strassen points out, there is a closer relationship between the cells of the metazoan body and the protozoa, which are not improbably the direct ancestors of these cells. Were the protozoa social in their behavior, did the different behavior of the several castes depend upon mutual interaction as it does to a certain degree among social insects, the analogy between behavior and development would indeed be close.

REFERENCES

ALLEN, B. M. The origin of the sex cells of Amia and Lepidosteus. Jour. Morph. 22, 1, 1911.

HARRISON, R. G. The outgrowth of the nerve fiber as a mode of protoplasmic movement. Jour. Exp. Zool. 9, 787, 1910.

HOLMES, S. J. (1) Observations on isolated living pigment cells from the larvæ of amphibians. Univ. of Calif. Pubs. Zool. 11, 143, 1913. (2) Behavior of ectodermic epithelium of tadpoles when cultivated in plasma. l. c. 11, 155, 1913. (3) The movements and reactions of isolated melanophores of the frog. l. c. 13, 167, 1914. (4) The behavior of the epidermis of amphibians when cultivated outside the body. Jour. Exp. Zool. 17, 281, 1914.

LOEB, J. On the heredity of the marking in fish embryos. Biol. Lectures, Marine Biol. Lab. Woods Hole, 1899.

MASSART, J., and BORDET, C. Recherches sur l'irritabilité des leucocytes, etc. Jour. Soc. Roy. Sci. Med. et Nat. de Bruxelles, 1890.

OPPEL, A. Causal-morphologische Studien. IV Mitteilung. Arch. f. Entw-mech. 34, 133, 1912; V Mitteilung, l. c. 35, 371, 1912.

PETERS, A. Ueber die Regeneration des Epithels der Cornea. Arch. mikr. Anat. 33, 153, 1889.

ROUX, WM. Ueber den Cytotropismus der Furchungszellen des Grasfrosches. Arch. f. Entw-mech. l, 1894.

WILSON, H. V. (1) Development of sponges from dissociated tissue cells. Bull. Bureau Fisheries, 30, 1911. (2) The behavior of the dissociated cells in Hydroids, Alcyonaria, and Asterias. Jour. Exp. Zool. 11, 280, 1911.

ZUR STRASSEN, H. Animal behavior and development. Proc. 7th Internat. Zool. Congress, Boston, 1912.

XI

THE INSTINCT OF FEIGNING DEATH

THE so-called instinct of feigning death is one which is very widely distributed in the animal kingdom. It crops out sporadically, as it were, in forms which are but very distantly related, and hence it must have been independently evolved a great many times. The expression feigning death is a misleading one to the extent that it is apt to give rise to the idea that the animal consciously adopts this device with the intent to deceive. But while it is probable that among the higher animals which sometimes feign death there may be an attempt to mislead their enemies, it is quite certain that among the insects, spiders and other low forms, there is no such aim in the creature's mind, if we grant (what some naturalists are disposed to deny) that these animals have minds. The unpremeditated character of this peculiar behavior was first shown by the experiments of Fabre on beetles. In order to ascertain if the duration of the feint was in any way affected by his own movements, Fabre made several observations on a large carab beetle, Scarites, which shows the death feigning instinct in a pronounced and typical form. When handled, the beetle would throw itself into an immobile state with its head bent down and its legs drawn in close to the body. It would remain in this attitude perfectly quiet for several minutes—sometimes for over an hour. Its awakening would be first manifested by a slight trembling of the feet and a slow oscillation of the antennæ and palps; then its legs would move about more vigorously, and finally the insect would arise and scamper off. Seized again, it would repeat the performance several times in succession, the duration of the feint often increasing with successive trials. Finally, as if wearied, or convinced that the ruse were vain, the beetle would refuse to feign longer.

Were the feints attempts to deceive its captor by simulating death? Fabre placed the insect on its back, went to a distant part of the room, and remained perfectly quiet. The beetle still lay as usual. He then went out of the room, carefully looking in at intervals to watch the course of events. Still the same immobility. In other cases he covered the insect so that it could not see out and then quietly went away. This was also found to make no difference. In fact, whether the insects were surrounded by sounds and sights of moving objects, or entirely excluded from these influences made no difference in the average length of time they would remain in a motionless condition. Similar experiments have been made on other insects by different observers, who have all arrived at the conclusion that conscious deception plays no part in the process.

The attitudes assumed by insects and other forms when feigning death are usually quite different from those of dead specimens. This general fact was pointed out by Darwin, who says that "I carefully noted the simulated positions of seventeen different kinds of insects (including an Iulus, spider and Oniscus) belonging to distinct genera, both poor and first-rate shammers; afterward I procured naturally dead specimens of some of these insects, others I killed with camphor by an easy slow death; the result was that in no instance was the attitude exactly the same, and in several instances the attitudes of the feigners and of the really dead were as unlike as they possibly could be."

The attitudes of animals in the death feint are frequently very characteristic. Many beetles as well as other forms feign with the legs drawn up to the body and the antennæ closely appressed, so that the whole insect assumes as compact a form as possible. The woodlouse, Armadillo, rolls itself up into a ball with its legs drawn into the center, a habit which has doubtless caused the name pill-bug to be given to this crustacean. A beetle, Geotrupes, according to Kirby and Spence, "when touched or in fear sets out its legs as stiff as if they were made of iron wire—which is their posture when dead—and remaining motionless thus deceives the rooks which prey upon them. A different attitude is assumed by one of the tree-chafers probably with the same end in view. It sometimes elevates its posterior legs into the air, so as to form a straight vertical line, at right angles with the upper surface of its body."

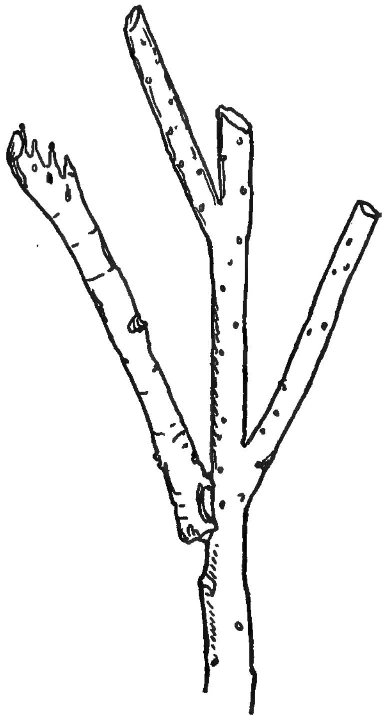


Fig. 8.—Larva of a geometrid moth attached to a twig.

Spiders usually feign by folding up their legs, dropping down, and remaining motionless. The caterpillars of some of the geometrid moths have the curious habit of attaching themselves to a branch by their posterior legs and holding the body straight and stiff at an angle to the stem, thus forming a remarkably close resemblance to a short twig. Frequently the deceptiveness is increased by a marked similarity in color to that of the branch to which they are attached.

While in most cases a species has a particular at-

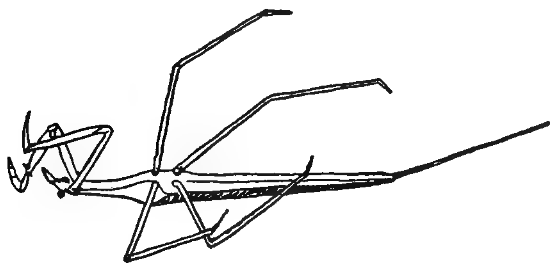


FIG. 9.—A water scorpion, *Ranatra,* feigning death.

titude which it maintains when simulating death, there are some forms which feign in whatever posture they may be when disturbed. A good example of this is afforded by the water-scorpion Ranatra. This insect has the two hinder pairs of legs, which are employed in walking and swimming, very long and slender; the first pair are fitted for grasping the small aquatic animals on which it feeds and are carried straight out in front of the body. It is only necessary to pick one of these insects out of the water to throw it into a stiff, immobile condition which usually lasts several minutes and sometimes for over an hour. The legs may be closely pressed to the body so that the creature resembles a stick, or they may stand out at right angles to it, or be bent in any position, some in one way and some in another, depending upon how they happen to lie when the feint began. And no matter how awkward the position, it is rigidly maintained until the feint wears off. I have found that young Ranatras, the first day they emerged from the egg and while their appendages were still soft and easily bent, showed the same death feigning instinct as the adults, although they did not persist in it for so long a time.

The water-bug Belostoma usually feigns with the legs closely pressed to the thorax or else held folded at right angles to the body. In Nepa, on the other hand, the attitudes assumed seem to depend mainly on the position of the legs just previous to the death feint, so that it is difficult to distinguish a feigning individual from one that is really dead. Schmidt has been able to make the walking-stick Carausius feign in all sorts of ungainly positions which would often be maintained for hours at a time.

Death feigning does not seem to occur among the lower invertebrate animals such as the Protozoa, cœlenterates, molluscs and worms, although some of them may exhibit reactions which are prophetic of this instinct. Among crustaceans the instinct in its fully developed form is quite uncommon. Some years ago I described the death-feigning of certain species of terrestrial amphipod crustaceans which are frequently found on sandy beaches near the seashore. On account of their peculiar hopping movements these crustaceans are commonly known as sand-hoppers or sand-fleas, although they have of

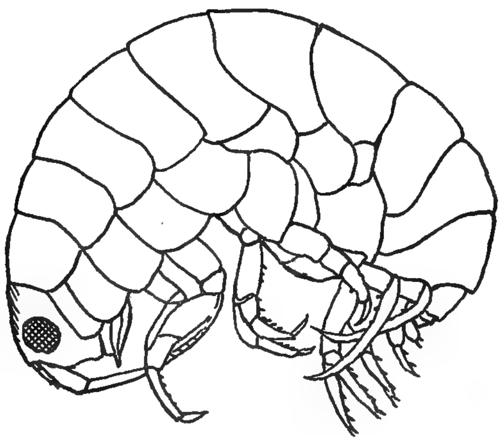


FIG. 10.—A sand flea, *Talorchestia,* in the death feint.

course no relation to the ordinary fleas of human experience. One of the largest species of sand-hopper, Talorchestia, is common along our Atlantic coast, where it lives during the day in burrows made in the sand, coming out only at night to feed upon the seaweed and other material washed ashore by the waves. When the Talorchestias are dug out of their burrows, they usually lie curled up with their long antennæ bent under the body and their legs drawn up so as to assume a compact form. They will lie in this way for several minutes, when they may be seen slowly to relax; the legs then move about, and soon the creature hops away by a sudden extension of its abdomen. When caught in the hand they will feign death again, and repeat the performance many times in succession. Other species of sand-hoppers exhibit the same instinct, though less perfectly, and there are traces of it in many of the reactions of their aquatic relatives.

The various species of wood lice exhibit the instinct of feigning death in various degrees. Some species are able to roll up into an almost perfect ball and will remain in that state for a considerable time. Other species curl up, but make only a very imperfect approximation to a sphere, and they may maintain this attitude for only a short period. Some myriapods when disturbed curl up in much the same way. Among spiders death-feigning is not uncommon, especially among the orb weavers.

It is among the insects that the death-feigning instinct reaches its fullest development, occurring to a greater or less extent in most of the orders. It is especially common in beetles and not unusual among the bugs, but it is quite rare in the highest orders such as the Diptera and the Hymenoptera, or the ants, bees and their allies. It occurs in a few cases among butterflies and moths, both in the imago as well as the larval state. The instinct is exhibited in different species in all stages of development from a momentary feint to a condition of intense rigor lasting for over an hour.

Among the vertebrate animals death-feigning has been observed only rarely in the fishes. In the Amphibia it is not exhibited in the striking way it occurs in insects and spiders, although frogs and toads may be thrown by the proper manipulation into an immobile condition more or less resembling it. A phenomenon apparently related to the death feigning of insects has long been known in certain reptiles. Darwin in his *Journal of Researches* describes a South American lizard which when frightened "attempts to avoid discovery by feigning death with outstretched legs, depressed body, and closed eyes; if further molested it buries itself with great quickness in the loose sand." The Egyptian snake charmers by a slight pressure in the neck region are able to make the asp suddenly motionless so that it remains entirely passive in the hands of the operator. And similar phenomena have been found in other species.

In birds the instinct crops out only here and there. A few summers ago when on the island of Penikese I was somewhat surprised to find the instinct well developed in the young terns which were hatched out in abundance on the hillsides. For a short time after being hatched the little downy fellows betray no fear of man and will cuddle under one's hand in perfect confidence. When the birds become larger and acquire their second coat of feathers the instinct of fear takes possession of them and they run and hide in the grass when you approach. Here they lie perfectly quiet; you may pull them about, stretch out their legs, necks, or wings and place them in the most awkward positions, and they will remain as limp and motionless as if really dead. They will even suffer their wing or tail feathers to be plucked out one by one without a wince. But all of a sudden the bird becomes a very different creature. It screams, pecks and struggles to escape, and is very apt to succeed on account of the surprising quickness of the change. I have made several attempts to make a bird feign death a second time, but never met with success.

According to Couch the land rail and skylark feign death, and Wrangle states that the wild geese of Siberia have the same habit during their molting season, when they are unable to fly. Hudson states in his most interesting *Naturalist on the La Plata* that the common partridge of the pampas, when captured, "after a few violent struggles to escape drops its head, gasps two or three times, and to all appearances dies. If, when you have seen this, you release your hold, the eyes open instantly, and with startling suddenness and noise of wings, it is up and away and beyond your reach forever."

In mammals the instinct is so well shown in one of the lower members of the group, the opossum, that the expression "playing possum" is familiar to every one. Foxes when trapped or hard pressed often drop down limp and apparently lifeless and will even endure a good deal of maltreatment without making any response. Hudson records that he was "once riding with a gaucho when we saw, on the open level ground before us, a fox not yet fully grown standing still and watching our approach. All at once it dropped, and when we came up to the spot it was lying stretched out, with eyes closed, and apparently dead. Before passing on my companion, who said it was not the first time he had seen such a thing, lashed it vigorously with his whip for some moments, but without producing the slightest effect."

Mr. Morgan in his book on the beaver gives the following instance on what he assures us is excellent authority: "A fox one night entered the hen-house of a farmer, and after destroying a large number of fowls, gorged himself to such repletion that he could not pass out through the small aperture by which he had entered. The proprietor found him in the morning sprawled out upon the floor apparently dead from surfeit; and taking him up by the legs carried him out unsuspectingly, and for some distance to the side of his house, where he dropped him upon the grass. No sooner did Reynard find himself free than he sprang to his feet and made his escape." Dogs are frequently deceived by this ruse of the fox and doubtless foxes have many times owed their lives to its aid. It has been often noticed that if one withdraws from a fox when it is feigning it may be seen to slowly open its eyes, then raise its head and carefully look around to see if its foes are at a safe distance, and finally scamper off.

While in insects the instinct of feigning death is probably a simple reflex reaction to outer stimuli, it is doubtless associated in birds and especially mammals with a tolerably acute consciousness of the situation. It involves a more or less deliberate intention to profit by the deception, yet at the same time it is probably not a result of conscious reflection. The instinct is there, or else such a course of action would not occur to the animal's mind. Were it otherwise it would be difficult to understand why the ruse is adopted only by certain species while many others, equally intelligent and for whom it would be an equally advantageous stratagem, never manifest it. There can be little doubt that a fox which slowly opens its eye and warily looks around is acting with an intelligent appreciation of his predicament, but it is not to be inferred that he could have reasoned out his course of action did not an innate proclivity in that direction form a part of his instinctive make-up.

The physiological condition in what is called death-feigning is quite different in different forms. While there is a general relaxation of the musculature in the sham death of some of the birds and mammals, the feint in most of the lower animals is characterized by a tetanic contraction of the muscles. The attitudes assumed by many forms, such as rolling into a ball, keeping the legs and other appendages drawn close to the body, or, in some cases, holding them straight and rigid, are such as can be maintained only at the cost of considerable muscular effort. If a Ranatra is picked up by one of its slender legs it may be held out horizontally for a considerable time without causing the leg to bend. The situation is similar to that of a man seized below the knee and held out straight, face upward, without causing the knee to bend. As the legs of Ranatra are relatively exceedingly slender, the muscular tension which the insect maintains must be intense. Similar muscular rigidity is shown in the walking-stick Carausius studied by Schmidt. Specimens supported by the tip of the abdomen and the ends of the outstretched fore legs would lie straight as a stick for hours.

Death feigning is markedly influenced by external conditions such as light, contact, moisture and especially temperature. In experimenting with amphipods I have found that when the temperature is lowered the death feint persists for a considerably longer time. The same is strikingly true of the death feint of Ranatra. At temperatures higher than the normal the Severins found that the duration of the death feint in the water bugs Nepa and Belostoma was greatly decreased. A sudden transition from a warm to a cold temperature, however, was found to diminish the duration of the feint in both of these species, owing possibly to the shock effect of the sudden change.

The influence of light on the duration of the feint has been studied by the Severins in the forms just mentioned and by myself in the water bug Ranatra. The results agree in showing that the duration of the feint is greater in dim than in strong light, and that the feint is further shortened if a light is kept moving over the insect. The latter result, like the former, is probably due to the greater stimulation to which the feigning insect is subjected. As all these water bugs are positively phototactic, light tends to elicit an active response which antagonizes the instinct of feigning death. In a Ranatra which is induced to come out of the death feint by moving a light above it, the first signs of life manifested are orienting movements of the head which take place in perfect unison with the movements of the light. These are followed by swaying movements of the body, until finally the insect attempts to follow the light by walking or, if highly excited, by flying.

It is a curious fact that while the water bugs, Nepa, Belostoma and Ranatra, feign death very readily when out of the water, they will do so much less readily when submersed in their natural element. In Ranatra repeated manipulations under the water usually fail to elicit anything but a momentary and undecided response. Nepa under the same circumstances feigns for a somewhat longer time, and Belostoma, in exceptional cases, may feign for as much as a few minutes. Throwing any of these insects into water while they are feigning usually terminates the feint at once or in a short time. The transition from air to water, even when no temperature changes are encountered, produces a marked effect on the reactions of many semi-aquatic forms. In Ranatra and certain terrestrial amphipods, as we have seen in a previous chapter, it produces a sudden reversal of phototaxis, a change not improbably due to the influence of contact stimuli. It is not improbable that it is the influence of contact stimulation that terminates the death feint of aquatic bugs when they are placed in the water.

Most insects and crustaceans which feign can be caused to do so repeatedly by stroking or handling them as soon as they show signs of activity. I have performed a number of experiments on amphipods, Ranatra, beetles and orb-weaving spiders to ascertain how long the death feint may be continued, and to determine also the lengths of successive feints. In all the forms experimented with there was found to be much variability in the behavior of different individuals, so that it was necessary to perform numerous experiments in order to arrive at trustworthy conclusions. In general, all the forms studied showed a gradual diminution in the duration of successive feints, until, often after several hours, it was no longer possible to evoke the response. Similar experiments undertaken at my request by the

Severins showed the same phenomenon in Nepa and Belostoma. Fabre in his studies on Scarites found an increase in the duration of the first five feints, but his observations were not sufficiently numerous to eliminate the rather large amount of variability due to unknown causes.

As the feints grow shorter the attitudes of the organism become less characteristic. Amphipods and pill-bugs do not roll up so completely or keep the appendages drawn so closely to the body. Spiders and beetles do not assume so compact a form, and in general it may be said that the muscular system gives evidence of diminished contraction. As the death feint is usually accompanied by a tetanic contraction of the muscles one would expect to find a diminution in the duration and perfection of the response as a simple consequence of fatigue. In a similar manner the diminution of the duration of the feint that occurs under higher temperature may be due to the fact that the muscles become exhausted more quickly when the metabolism is increased by the higher temperature of the body.

The experiments undertaken to ascertain what part of the nervous system is most concerned in the death feint have yielded somewhat varied results. Robertson found that in the active species of spiders Epeira and Amaurobius the sham death reaction persisted after the removal of the brain, and was manifested in a weakened form when the subesophageal ganglion and even the first thoracic were removed also. In a sluggish spider Celænia Robertson found that "The sham death posture cannot be induced without the head ganglia." Schmidt finds that in Carausius the death feint entirely disappears after the removal of the brain. My own experiments on Ranatra showed that removal of the brain caused a marked diminution in the duration of the feint, although the response could still be induced in decerebrate specimens. If a feigning individual be cut in two across the prothorax the posterior part often continues to retain its rigidity for some time and may be thrown back into the death feint again if it is picked up and stroked. Similar results were obtained in Belostoma and Nepa by the Severins, who have investigated the rôle of the nervous system in especial detail. The cataplectic state which Preyer and Verworn found could be induced in decerebrate fowl may be allied to the conditions described above.

One marked characteristic of the death feint is an apparent insensibility to pain. De Geer in writing of a boring beetle *Anobium pertinax* says that "you may maim them, pull them limb from limb, roast them over a slow fire, but you will not gain your end; not a joint will they move, nor show by the least symptom that they suffer pain. A similar apathy is shown by some species of saw-flies (Serrifera), which when alarmed conceal their antennæ under their body, place their legs close to it, and remain without motion even when transfixed by a pin. Spiders also simulate death by folding up their legs, falling from their station, and remaining motionless; and when in this situation may be pierced and torn to pieces without their exhibiting the slightest symptom of pain." The Severins tried the application of heat to Belostoma, but the insect was invariably brought out of its feint and made struggles to escape, although it might endure more or less mutilation without making any response. I have found that a feigning Ranatra will allow its legs to be snipped off without betraying the least movement beyond an occasional twitch. Similar insensibility has been observed in Nepa (Severin), Carausius (Schmidt) and other forms.

As has been pointed out by Romanes, Preyer, Verworn, Schmidt and others, the instinct of feigning death is doubtless closely connected with much of what has been called hypnotism in the lower animals. Crayfishes, frogs, lizards, certain snakes and many birds and mammals, may by a very simple process be thrown into an inactive condition from which they are not readily aroused by external stimuli. In ordinary death feigning the animal falls into its immobile state upon slight provocation; a touch, or even a jar is sometimes all that is required. In the so-called cases of hypnosis more or less manipulation is necessary. The exciting cause in both cases is generally some form of contact stimulus. In the hypnotism of animals, as Verworn and others have shown, there is diminished reflex irritability, and usually tonic contraction of many at least of the muscles. Similar phenomena are observed in the death feigning of many forms, some of the insects, as we have seen, showing a lack of responsiveness that is truly remarkable.

The independent development of death feigning along many different lines of descent makes it probable that we must look for the origin of this curious instinct in some fundamental and widespread mode of behavior. In a paper on the death feigning of terrestrial amphipods the writer has suggested that the death-feigning instinct in these forms had its origin in an accentuation of the thigmotactic response which is such a prevalent trait of behavior among the amphipods in general. It was found possible to establish a series of stages between the typical death feint of the large terrestrial amphipod Talorchestia and the ordinary thigmotactic reactions of the aquatic relatives of this species. In *Orchestia palustris,* a species not so exclusively terrestrial as the preceding, the body during the death feint is less closely curled up, the appendages are not so closely drawn up to the body, and the feint is not so persistent. In the small *Orchestia agilis,* which lives usually near the water line, the death feint is shown in a somewhat less decided way, while among the aquatic members of the Orchestiidæ the same trait is manifested by a tendency to curl up and lie quiet when in contact with rocks or seaweed. To one who has studied and compared the attitudes and behavior of this series of forms there can be little doubt that the typical death feint of the most terrestrial of the species has its basis in the thigmotaxis of the aquatic forms. As the species studied become more terrestrial in habit, the thigmotaxis becomes gradually specialized into a typical instinct of feigning death.

Many facts indicate that death feigning in insects and other forms has had a similar origin in the thigmotactic response. It is a rather striking fact that, with very rare exceptions, it requires some form of contact stimulus, it may be but a touch, jar, or even a breath of air, to elicit this instinct. One of the very few exceptions to this rule which has been recorded is afforded by Carausius, whose death feint, according to Schmidt, arises from internal causes, and cannot be induced by any discoverable environmental agency. Should it be definitely established that this case is truly one of "autocatalepsy," as it has been called by Schmidt, it would not be fatal to the supposition that it began originally as a reaction to contact; for it is not without precedent that an instinct having originated with reference to one feature of the environment should finally come to be set into operation by a quite different cause.

Those cases of death feigning in which there is a limp and relaxed condition of the musculature, such as occurs in some birds and mammals, may have an origin quite different from that of the more prevalent cataleptic type. The suggestion that death-feigning had its origin in the partial paralysis produced by fear may perhaps apply to cases such as these, although this explanation cannot, I feel sure, be extended to the derivation of the typical form of this instinct. While there is simulation of death in both types of behavior we have described, it is probable that we have to do with two distinct kinds of reaction differing both in their physiological character and in their phyletic origin.

REFERENCES

DARWIN, C. Chapter on instinct appended to Romanes' mental evolution in animals. 1884.

FABRE, J. H. Souvenirs entomologiques, T. 7.

HOLMES, S. J. (1) Death feigning in terrestrial amphipods. Biol. Bull. 4, 191, 1903.

(2) Death feigning in Ranatra. Jour. Comp. Neur. Psych. 15, 200, 1906.

(3) The instinct of feigning death. Pop. Sci. Mon. 72, 179, 1908.

HUDSON, W. H. The naturalist on the La Plata, 1892.

KIRBY, W. and SPENCE, W. An introduction to entomology. 6th ed., 1846.

LÖHNER, L. Untersuchungen über den sogenannten Totstellreflex der Arthropoden. Zeit. allg. Physiol. 16, 373, 1914.

MORGAN, L. H. The American beaver and his works, Phila. and London, 1868.

POLIMANTI, O. Studi di Fisiologia etologica. II, Lo stato di immobilita temporanea ("morte apparente"-"Totenstellen") nei Crostacei Brachiuri. Zeit. allg. Physiol. 13, 201, 1912.

ROBERTSON, T. B. On the "sham-death" reflex in spiders. Jour. Physiol. 31, 410, 1904.

ROMANES, J. G. Mental evolution in animals. 1884.

SEVERIN, H. H. P., and SEVERIN, H. C. An experimental study on the death-feigning of Belostoma (-zaitha aucct.) flumineum Say and Nepa apiculata Uhler. Behavior Monographs, Vol. I, No. 3, 1911.

SCHMIDT, P. Katalepsie der Phasmiden. Biol. Cent. 33, 193, 1913.

VERWORN, M. (1) Tonische Reflexe. Arch. ges. Physiol. 65, 63, 1897.

(2) Beiträge zur Physiologie des Zentralnervensystems. I Teil. Die sogenannte Hypnose der Tiere. Jena, 1898.

XII

THE RECOGNITION OF SEX

HOW do the males of the lower animals distinguish the females of their own species from all the rest of the animate creation? Obviously the perpetuation of the race depends on the circumstance that the male is correctly guided in the choice of a mate. A male beetle or bug will pass by with indifference thousands of other varieties of insects, but in the presence of a female of his own kind his interest is keenly aroused. It almost goes without saying that this power of discrimination is a matter of instinct. It is easily demonstrable in most animals that the element of experience is entirely unnecessary for the proper solution of this important problem. Apparently the male is guided by a sort of elective affinity to the right object upon which to bestow his attentions. What are the signs by which this object is recognized?

An important factor in the discrimination of sex that naturally occurs to one is the sense of smell. The lower animals, or at least many of them, are influenced by odors to an extent which we with our comparatively obtuse olfactories find it difficult to appreciate. The odors of most species are specific, and even individuals, in higher forms at least, have an odor peculiarly their own which a bloodhound is able to distinguish from among dozens of others. Differences in odor frequently characterize the two sexes, and hence afford a feasible means of sex discrimination.

The males of many forms have much more highly developed olfactory organs than the females. The antennæ of insects which contain the olfactory sense organs are frequently larger and more complex in the males. In the drone bee, for instance, the olfactory pits of the antennæ are many times more numerous than in the queen or worker. Many male moths have large feathered antennæ, whereas these organs are much smaller in the females. It is mainly through the sense of smell that the male moths are able to find their mates, and in some species this sense is developed to a degree that almost surpasses credence.

In one of his most delightful essays the French naturalist Fabre tells of the nuptial flight of the males of the large and beautifully colored moth called the great peacock (*le grand paon*). A cocoon which was kept in Fabre's study had produced a female moth which was placed under a gauze cover. In the evening the observer had his attention attracted by the call of his young son: "'Come quick, come and see these butterflies! Big as birds! The room is full of them!' Several of the large moths had come into the room through the open window.

Others had entered the kitchen, and still others were found in various rooms wherever there was a chance for them to enter. . . .

"It was a memorable night—the Night of the Great Peacock! Come from all points of the compass, warned I know not how, here were forty lovers eager to do homage to the maiden princess that morning born in the sacred precincts of my study." The night was one of black darkness, yet the moths threaded their way through the trees surrounding the house, and came through open windows into darkened rooms without abrading in the least the scaly covering of their wings. But keen as the sense of sight in these insects may be it is not through this sense that the males are drawn toward their intended mates. "When," says Fabre, "I placed the females in boxes which were imperfectly closed, or which had chinks in their sides, or even had them in a drawer or a cupboard, I found the males arrived in numbers as great as when the object of their search lay in the cage of open work freely exposed on a table. I have a vivid memory of one evening when the recluse was hidden in a hat-box at the bottom of a wall-cupboard. The arrivals went straight to the closed doors, and beat them with their wings, *toc-toc,* trying to enter. Wandering pilgrims, come I know not where, across fields and meadows, they knew perfectly what was behind the doors of the cupboard."

Fabre cut off the antennæ of several of the males of this and other species of moths and found that they failed to approach the vicinity of the female. The presence of other odors, which would make an almost intolerable stench in our own nostrils, failed to deter the males in the least from the object of their search. The odor, according to Fabre, seemed to be carried against currents of air, for a rare female specimen of the Lesser Peacock drew numerous males which flew *with the wind* to the place of her confinement. It is scarcely to be wondered at that Fabre considered the sense of smell to depend in part on other means than the wafting of odorous particles, a sort of force acting after the manner of rays of light or X-rays and capable of radiating to a great distance despite adverse currents of air.

The rôle of smell in sex recognition among the crustaceans is more uncertain. The antennal sense organs which are very probably olfactory in function are in some species much better developed in the male sex. But little is known, however, in regard to the means by which most species find their mates. In some amphipod crustaceans with which the writer experimented a few years ago olfactory stimuli were found to play little or no part in the discrimination of sex. The males of this group have the curious habit of carrying the females about under the body. This act of transportation has no direct reference to the impregnation of the eggs further than to insure the proximity of the sexes when the proper time for fertilization arrives. This occurs soon after the female casts off her skin, when the sperms are deposited by the male on the ventral side of the thorax of his mate. After the eggs are fertilized the male continues to swim about with the female as before.

"The instinct of the male amphipod [1] to seize and retain hold of the female is one of remarkable strength. The male retains his hold, despite all efforts to dislodge him, with remarkable persistence, and will still cling to the female after the posterior half of his body has been cut away. My own observations on the sexual behavior of amphipods relate mainly to three species, *Amphithœ longimana* Smith, *Hyalella dentata* Smith, and *Gammarus fasciatus* Say. The sexual behavior of these three species is remarkably similar although they belong to as many distinct families. The female while carried about keeps remarkably impassive. Her thoracic legs are drawn up, the abdomen held strongly flexed, the whole body assuming as compact a form as possible. She takes no part in swimming; the movement of the pleopods when the body is strongly bent upon itself serves only to keep a current of water passing by the gills. She is carried about like a helpless burden, allowing her vigorous spouse to assume the entire labor of transportation and the responsibility for keeping her as well as himself out of danger.

"The efforts of the male to seize the female and get her into the proper position to be carried have the effect of inducing her to throw herself into the

[1] Quoted from an article by the writer on "Sex Recognition in Amphipods," published in the Biological Bulletin, Vol. 5, p. 288, 1903.

characteristic bodily attitude and remain quiet. The attitude assumed by the female is similar to that observed in the ordinary thigmotactic reaction of amphipods and may, perhaps, be but the same form of response somewhat modified and specialized in relation to the function of reproduction. When the males are torn away from the females they soon seize their partners again and roll them about into the proper position and then proceed on their way in apparent contentment. The female, as soon as seized by the male, curls up and allows herself to be rolled and tumbled about without a show of resistance or protest. The males, as a rule, are larger than the females and usually get their partners into the desired position quite readily; but when a small male attempts to carry a large female he experiences much difficulty. I observed a male Hyalella endeavoring to carry a female somewhat larger than himself. After seizing the female he would turn her around until she finally came into the proper position for transportation, but owing to the larger size of his partner the male could not reach around her body so as to carry her away. No sooner was the female properly adjusted than the male would lose hold of her round body and the same efforts had to be repeated. During all this performance the female remained dutifully passive. After watching the further struggles of the male for over half an hour I became convinced, although he was not, that he had undertaken an impossible task, and discontinued my observations."

That the male amphipods do not distinguish the females by sight was shown by blacking over the eyes of several males and then placing them in a dish with females. It was not long before each male had secured a mate. The possible rôle of the sense of smell was tested by removing from a number of males the first antennæ which contain the olfactory sense organs. After the specimens had recovered from the slight shock of the operation they seized the females and carried them about in the usual manner. They reacted in the same way when the second antennæ were removed also.

In another experiment several females were confined within an enclosure of wire gauze which was placed in a dish of water containing several eager males. The males paid not the slightest attention to the females within the enclosure, but after it was raised and the females allowed to scatter through the dish, most of the males were found carrying their mates.

"If one attentively observes Hyalellas as they are swimming about, it will be seen that the males do not pursue the females, great as their eagerness may be to seize and carry one of the opposite sex. Only when the two sexes collide in their apparently random movements does the male become aware of the presence of the female. When a male and a female collide, the female curls up and lies quiet while the male makes efforts to seize her. Should two females collide they may curl up for a moment, but as they are not seized they soon pass on. When two males meet there is often a lively struggle. Each apparently attempts to seize and carry the other, but as neither will consent to remain passive they soon separate. The different reactions of the two sexes to contact with other individuals is the factor which effects the union of the males with the females. Each reacts to the reactions of the other. The male has a strong instinct to seize and carry other individuals of the same species. The female has the instinct to lie quiet when another individual comes into contact with her, especially if she is seized. The instinctive reactions of the two sexes are complementary, and coöperate to bring about and maintain the peculiar sexual association characteristic of the Gammaridea.

"If the association of the sexes is brought about by their peculiar modes of reaction to certain contact stimuli, it would seem probable that the only reason why males do not carry other males as well as females is that they are prevented from so doing by the active resistance of their intended mates. I was accordingly led to try the experiment of mutilating some male specimens so that they could no longer make effective resistance to seizure. The large second gnathopods (the principal means of defense) of several males were cut off and the mutilated individuals were placed in a dish with several males which were recently torn from females. The mutilated males were soon seized and carried about as if they were members of the other sex. In one case a mutilated male was carried about for over five hours. The mutilated males were more active than females are under the same conditions, and did not assume the same bodily attitude, but nevertheless their captors carried them without any manifest awareness of the deception to which they were subjected."

In another group of crustaceans, the Copepoda, the mating instincts are more or less analogous to those of the amphipods. In the copepods, however, the males in seizing the females employ the first antennæ, which are often enlarged and especially modified for this function. In *Cyclops fimbriatus,* whose behavior was studied by the writer, the male clasps the female just in front of an enlargement at the base of the abdomen. Males show much eagerness in grasping the females, and they may be poked about roughly with a needle and the posterior part of the body may be cut off without causing them to leave their hold.

"As the pairs of Cyclops [1] swim through the water the males are usually the more active. Frequently the female remains entirely quiet with the appendages drawn close to the body, and the body flexed ventrally, allowing herself to be passively carried about by her mate. At other times the female may swim as actively as the male. In general the be-

[1] Quoted from Holmes on "Sex Recognition in Cyclops," Biological Bulletin, Vol. 16, p. 313, 1909.

havior of the females and their attitude while being carried closely resemble what is found in the Amphipoda. So also does their behavior when the males come in contact with them and attempt to seize them. The female during the efforts of the male to clasp her around the base of the abdomen usually lies quiet with the appendages drawn close to the body. . . .

"So far as could be detected the males do not seek or follow the females at a distance as Parker concluded they did in Labidocera. The association of the sexes seems to be due merely to chance collisions. Males often attempt to seize other copepods regardless of sex. The males resist such attempts at seizure and dart quickly away, while the females often stop and submit readily to the clasping propensities of their companions. Several males were injured so that they could not resist seizure, and in many cases they were seized by other males who worked industriously until they got their burden clasped around the base of the abdomen in the usual way. These associations did not last long, however; the active males, apparently appreciating that something was wrong, soon swam away. Recently killed females were often seized and in some cases carried about for a while, but they were finally dropped."

There was no evidence that odor determined the sexual behavior of the males. The males paid no attention to a number of females that were enclosed within a tube whose end was covered with wire gauze. In another experiment several females were placed in a tube in which a small plug of loose cotton was inserted a short distance from one end. The males showed no tendency to enter the open mouth of the tube as they might be expected to do if they were attracted by the odor of the females. The experiment of removing the organ of smell, which was performed in the case of the amphipods, would be a fruitless one in Cyclops, as the seat of smell is located, to a considerable degree at least, in the same organs that are used for clasping.

"It is evident that mating in Cyclops is brought about much as it is in the Amphipoda. The males have a strong tendency to clasp other copepods; the females tend to remain quiet in a condition somewhat resembling the death feint while being seized by the males. It is not improbable that olfactory stimuli may cause the males to remain with the female longer than they otherwise would, and they may render the males more prone to seize females than other males, but so far as could be determined by watching the behavior of the animals the specific reaction of the two sexes to certain kinds of contact stimuli is the main factor in bringing about their association."

In the crayfish the studies of Andrews and of Pearse have shown that sex recognition is effected by much the same method as is followed in the amphipods. Extracts from the bodies of females added to water containing the males did not elicit the least response. Nothing in the behavior of the males indicates that they are drawn toward the females by the sense of smell. Mating apparently is dependent upon the chance meetings of the sexes. "During the mating season," says Pearse, "the instinct of the male is to grasp and turn over every crayfish that comes in his way. . . . If this individual is a female of the same species the attempt may meet with success, but if it is a male or a female of another species the effort at sexual union is usually of short duration." If males attempt to mate with other males, as they often do, they encounter active resistance, but if a female is attacked she usually remains passive.

In fishes the males are frequently distinguished by their more conspicuous coloration especially during the breeding season. The pugnacity and threatening attitudes of the males at this time undoubtedly contribute to their mutual recognition, but there is evidence that the mature males often recognize one another by their peculiar markings. In her account of the breeding habits of the rainbow darter, Miss Reeves records several cases of young dull-colored males being mistaken for females, whereas the larger and more brilliantly colored adults usually recognize one another without difficulty. "The more nearly the behavior of a dull male simulates that of a female, as in the case of a male burrowing for food, the more is he likely to be taken for a female. Upon the near approach of the brilliant male the young male erects the first dorsal and rapidly escapes, modes of behavior not observed in the female. It appears, then, that the brilliant fish distinguishes the two by their behavior; a mode of sex recognition pointed out by Holmes (1903) in the case of amphipods. In the case of very young males the sex recognition must be wholly of this character, while males which already show some little sexual coloration are probably distinguished upon near approach by means of it as well as by behavior." [1]

Among the amphibians the recognition of sex in the frog has been the subject of several interesting experiments by Goltz. In frogs and toads the males clasp the females during the breeding season until the eggs are discharged when the male sheds his sperm over them. What it is that induces the male to discharge his sperm at the opportune moment when the eggs are passing from the female has never been satisfactorily cleared up. The clasping of frogs insures that the male is on hand when his services in fertilizing the eggs are required. The clasping instinct is a temporary one, coming on early in the spring, and then ceasing after the short breeding period is past, when the sexes scatter and pay no further heed to one another's existence. As is well known, male frogs and toads often clasp various objects during the breeding season. Frogs have been found to clasp fishes the eyes of which they sometimes gouge out with their thumbs; and I have taken a male toad industriously clasping an old dried apple.

[1] *Biological Bulletin*, Vol. 14, p. 35, 1907.

The instinct to clasp is one of great strength and male toads may suffer their bodies to be cut in two without relinquishing their hold on the female.

Correlated with the appearance of the breeding instinct there occurs increased development of the inner digital muscles and certain other parts of the fore legs of the males, a development which Nussbaum has shown to be checked if the males are castrated a considerable time before the onset of the breeding season. Probably as a result of internal secretions of the reproductive glands, parts of the neuro-muscular mechanism become at this time peculiarly irritable, so that a particular form of reflex activity is very easily evoked. But notwithstanding this, a frog or toad seldom clasps for long anything but the female of his own kind. Other males may be clasped, but they are usually soon relinquished, while a female is clasped the more firmly the longer she is held.

How does the frog distinguish male from female? Goltz has found that blinded frogs discriminate between the sexes as well as normal frogs. After the olfactory nerves were cut he found that males can still distinguish females, so that neither sight nor smell is a necessary element in the recognition of sex. Even when the males were robbed of both sight and the sense of smell many of them succeeded in clasping the females among which they were placed. When the females were rendered mute by an operation they were no longer seized.

Males, Goltz concluded, are not drawn toward the females through one sense alone, but by means of several senses, no one of which is indispensable. It is a striking fact that a frog whose head is cut in two so as to remove the cerebral hemispheres and eyes will nevertheless continue to clasp a female that is presented to him, while he soon rejects one of his own sex.

The bodies of females are commonly plumper than those of the males. May the latter perchance distinguish the females by their form? Goltz tried the experiment of stuffing out the body of a male frog and giving it to another male, but he found that it was soon abandoned. Does the male frog have so delicate a tactile sense that even though nearly brainless he cannot be deceived as to which sex is within his grasp? Goltz is inclined to consider that such is the case. It may be open to doubt, however, if the possibility was sufficiently considered that sex recognition may be a result of the behavior of the two sexes, much as it was found to be in amphipods. Despite the interesting experiments of Goltz the matter requires further investigation before a decided conclusion can safely be drawn.

In the birds the sexes may often be easily distinguished by sight, and in many species each sex is doubtless able to recognize the other by this sense alone. The discrimination may be aided by the observation of differences in behavior. There is little evidence from the behavior of birds that the sense of smell is relied upon in this matter to any degree. In those birds in which the two sexes are much alike, as in most pigeons, differences in behavior apparently afford the chief means by which each sex distinguishes the other. Craig in his interesting account of the expressions of emotions in pigeons [1] says that "If a cage containing an unmated male ring-dove be suddenly brought alongside another cage containing another ring-dove, of unknown sex, the male becomes highly excited at once, and gives vent to his excitement in all possible ways. First he bows and coos with all his might, and he continues to do so for a long time. Then he charges about the cage, assuming the attitude peculiar to the charge, and frequently repeating the loud kah-of-excitement. At intervals he stops to glare at the strange bird and sometimes to peck at it through the bars, but soon he starts again to bow-and-coo and charge. . . .

"If left beside the stranger's cage for some hours, the male must sometimes rest and be silent; but even the intervals of rest and silence are broken frequently by series of perch-coos. This behavior on the part of the male is useful in that it stimulates the strange bird to respond, and, in responding, to reveal its sex.

"If the strange bird be a male, it shows similar

[1] *Journal of Comparative Neurology and Psychology,* Vol. 19, p. 29, 1909.

excitement and aggressiveness. And the two males are sure to fight if they can reach one another.

"But if the strange bird is a female, she acts far otherwise. She is at first very indifferent, unless she is particularly anxious to mate. And after some days, when she begins to show an interest in the male, she does not give the bowing-coo, nor charge up and down the cage, nor show other signs of pugnacity and aggressiveness. So far from tending to aggress the male, her conduct is rather an expression of submission to him. She shows a certain excitement; for instance when she utters the kah it is a kah expressive of gentle excitement. But she spends the greater part of her time in alluring the male by means of the nest-calling performance—the nest-calling attitude, seductive cooing, and gentle flip of the wings. She often tries to get through the bars of her cage to the male; and, failing to do so, she sometimes lies down with one side pressed against the bars. . . .

"When the male sees the strange bird behaving in this submissive and seductive manner, he loses the intensity of his pugnacity; though he always continues to be masterful. He spends less time now in the bowing-coo and more time in nest-calling and in trying to get to the female."

In the mammals the sense of smell plays a much larger part in the recognition of sex than it does in birds and the lower vertebrates. Not only is the sense of smell as a rule acute, but scent glands of various kinds are of frequent occurrence in one or both sexes, and frequently the secretion of these glands is exceptionally abundant during the breeding season. Commonly scent glands are better developed in the male sex. The strong odor of the male goat is notorious. In the male elephant there are glands on the side of the face which, in the breeding period, enlarge and emit a milky secretion. In the males of many species of deer and antelope there are facial glands that are especially active in the rutting season. Other species have scent glands on the feet and limbs, or near the tail.

It is not improbable that the secretion of these glands, while not particularly agreeable to ourselves, may have an alluring influence on the opposite sex of the species concerned. There is abundant evidence that different species of mammals are able to recognize their own kind through the sense of smell, and it is a well-known fact that many mammals are exceedingly quick to detect the scent of an approaching enemy. Any one who has watched the behavior of dogs in taking a sniff at their different acquaintances, or in getting a fuller olfactory impression of a stranger, will realize somewhat to how great an extent experience with odors makes up the dog's mental world. Many facts indicate that mammals distinguish the opposite sex of their own species through the sense of smell, but as the sexes frequently differ in external appearance they are undoubtedly able to recognize one another by sight. A certain familiarity with the habits of street curs will convince one, I think, that the element of behavior, as in some of the cases previously described, plays a certain rôle also.

The recognition of sex has been little analyzed in the mammals. The problem is more complex than in lower forms owing to the higher development of the mammalian mind, and the fact that several different senses are usually involved.

REFERENCES

ANDREWS, E. A. Conjugation in the crayfish, Cambarus affinis. Jour. Exp. Zool. 9, 235, 1911.

BANTA, A. M. Sex recognition and the mating behavior in the wood frog, Rana sylvatica. Biol. Bull. 26, 171, 1914.

CRAIG, W. The expression of emotion in the pigeons. I, The blond ring dove (Turtur risorius). Jour. Comp. Neur. Psych. 19, 29, 1909.

FABRE, J. H. Souvenirs entomologiques, 7 serie.

GOLTZ, F. L. Beiträge zur Lehre von den Funktionen der Nervenzentren des Frosches. Berlin, 1869.

HOLMES, S. J. (1) Observations on the habits of Hyalella dentata. Science, N. S. 15, 529, 1902. (2) Sex recognition among amphipods. Biol. Bull. 5, 288, 1903. (3) Sex recognition in Cyclops. Biol. Bull. 16, 313, 1909.

PARKER, G. H. Reactions of copepods to various stimuli, etc. Bull. U. S. Fish Com. 21, 103, 1901.

REEVES, C. D. The breeding habits of the rainbow darter (Etheostoma cœruleum Storer), a study in sexual selection. Biol. Bull. 14, 35, 1907.

XIII

THE RÔLE OF SEX IN THE EVOLUTION OF MIND

THE reason for the existence of sex is one of those biological problems whose solution seems as remote as it did a century ago. Many remarkable discoveries have been made in regard to the microscopic structure and development of the germ cells in both plants and animals. We have learned much of the general biology of sex, and the probable evolution of sex in the organic world. And substantial progress has been made with the old problem of the determination of sex. But to the question, Why came there to be two sexes at all? or in other words, Why do not organisms continue to reproduce asexually as it is probable they once did? we can only offer answers that, to say the least, are very hypothetical.

While the fact that sex is absent in the lowest forms of life indicates that evolution has proceeded at least a certain distance without its aid, and suggests the possibility of the evolution of sexless forms of a high degree of organization, yet the general prevalence of sex, with but rare exceptions, in all but the most primitive organisms points to the conclusion that sex has played a fundamental rôle in the evolution of the organic world. It is doubtless futile to conjecture what the organic world would have been like if the institution of sex had never been evolved. Even if the processes of variation and selection had gone on to the same extent—which is scarcely probable—the absence of sex would certainly have given to evolution a very different direction from that which was actually followed. Many of the most complex of the structural arrangements of organisms have especial reference to securing the meeting of the germ cells. The color and scent of flowers, and their many and beautiful adaptations to effect cross fertilization would never have appeared if plants were propagated solely by the asexual method. In animals the structural peculiarities associated with sex are, as a rule, among the most complex features of the body. Correlated with these structures we find mating instincts which frequently manifest themselves in complex modes of behavior. More acute senses have been evolved in many cases very largely in relation to securing the meeting of the sexes. The large antennæ of male moths and several other insects, the larger eyes of the common drone bee, and the auditory apparatus of the male mosquito are a few of the numerous illustrations of this fact.

The various kinds of apparatus in insects for making sounds which are found in crickets, locusts, and cicadas are devices for drawing the sexes together, and the complementary development of auditory organs in the same insects has doubtless been greatly furthered through the evolution of these structures. The primary function of the vocal apparatus of the vertebrates was probably to furnish a sex call, as is now its exclusive function in the Amphibia. Only later and secondarily did the voice come to be employed in protecting and fostering the young, and as a means of social communication. And the evolution of the voice in vertebrates doubtless influenced to a marked degree the evolution of the sense of hearing. It is not improbable, therefore, that the evolution of the voice, with all its tremendous consequences in regard to the evolution of mind, is an outgrowth of the differentiation of sex.

In cases of degeneration through parasitism or other causes the female often proceeds much farther on the downward path than the male. In the scale bugs, for instance, the females have lost their wings and many other structures, while the adult male remains an active and graceful winged insect. The necessity for finding the female has kept the male from undergoing the degeneration that has overtaken the other sex.

Much of the elaborate organization of the imago state of insects has reference to activities directly or indirectly concerned with mating and depositing the eggs in the proper environment for the development of the young larvæ. There is a relatively long nymphal or larval period chiefly devoted to the vegetative functions of assimilating nutriment, and growth; in many species the imago takes no food or need take none, before the eggs are fertilized and laid; and in several forms the mouth parts have become so atrophied that food taking is impossible. Some insects mate soon after they emerge from the pupal covering. In the May-flies, which live but a short time in the winged state in order to mate and deposit their eggs in the water, it is probable that the imago stage would long ago have disappeared were it not retained as a means of effecting the union of the sexes. So also with many other insects. In the winged state numerous new enemies are encountered and many lives are lost; in the pupa stage, which prepares for it, there is commonly an extensive tearing down of old structures and the building up of new ones during which the insect is helpless against many enemies and parasites. There are compensatory advantages in the possession of the imago stage in scattering the species into new regions, and in many other ways in the different groups, but were it not for the necessity for preserving the mating activities which occur in this period of the insect's life-history, it is probable that the complex organization of the adult state would very frequently have degenerated, or even been lost, if it had not failed to develop at all.

The mating activities are almost everywhere among the most complex performances of an animal's life. The opposite sex must be distinguished from all other creatures and responded to accordingly. Often pursuit and capture or winning over are the necessary preliminaries of mating. All this puts a premium so to speak on the sharpening of the senses, the development of strength and acuteness, and the evolution of higher psychical qualities. Consider the mating activities of crustaceans, the courtship of spiders, the breeding activities of fishes, and still more the elaborate wooing of male birds, and it will become manifest how greatly the institution of sex must have stimulated the evolution of more complex modes of behavior.

All the facts here cited are trite enough even to the non-biological reader. But while it is sufficiently evident that the differentiation of the sexes has promoted the development of behavior in relation to mating, it may be well to point to the enormous indirect consequence of this development in respect to the evolution of mind in general. In the evolution of behavior one kind of instinct grows out of another just as new organs are usually formed by the elaboration of some pre-existing structure. A general elaboration of instinctive reactions in regard to any one sphere of activity affords a basis, therefore, for the differentiation of more complex or specialized behavior in respect to other activities. The primary function of the voice, as has already been pointed out, was to serve as a sex call. Later it became the means of various instinctive forms of communication and finally afforded the medium of articulate language. Had it not been for its value in the mating of the lower vertebrates the voice might never have been evolved and man never have become man.

While the specialization of senses, which, in certain cases at least, has been carried on mainly for sexual purposes, naturally afforded a basis for the elaboration of many instincts, it is practically impossible to trace in detail how various instincts, sexual and other, may have acted and reacted on one another's development. But we can discern enough of the influence of sex differentiation on the evolution of behavior to feel assured of its importance. The necessity of solving the one problem that confronts all diœcious animals which do not simply shed their sexual products at random into the water has kept behavior in one sphere up to a certain minimum standard. The male must find and impregnate the female, and this fact sets a certain limit to his degeneration, at least in some period of his life. But besides acting as a check to degeneration, the necessity for mating has, in general, been a constant force making for the evolution of activity, enterprise, acuity of sense, prowess in battle, and the higher psychic powers. We cannot pretend accurately to gauge its rôle in the evolution of mind, but it has evidently been a factor of enormous potency.

XIV

THE MIND OF A MONKEY

LIZZIE was first seen in a store on Market Street, San Francisco, where she was confined in a cage with a small puppy which was put in for company. She was a specimen of bonnet monkey, *Pithecus sinicus,* and she had been recently imported from India, so her owner averred, but during her short captivity she had come to be quite tame and tractable. A few days later she became the property of the University of California, and was kept in a cage especially constructed for her reception in a sort of storeroom belonging to the department of zoology. Owing perhaps to the strangeness of her new surroundings, or to the loss of her old associates, Lizzie frequently gave vent to a plaintive cry, but she seemed to be appeased when any one came near. When let out of her box she began to scamper about, climbing up tables and other objects, and examining things critically all about the room. If approached she would often utter a sound resembling a bark and stand with her mouth open in a threatening attitude, at the same time being on the alert to make her escape. She proved to be remarkably agile, even for a monkey, and very quick to discover the least movement anywhere within her range of vision. She would move about almost constantly, but her attention was not directed to any one object for more than a few seconds at a time.

Lizzie showed a strong aversion to being taken in the hands, although she soon came to jump upon my shoulder and ride about there quite contentedly. Often when I stretched out my hands to seize her she would bound past them to my arm and quickly scamper to my shoulder. It was difficult to get hold of her in that situation, for she would clamber about over my body in a very nimble way in her efforts to avoid seizure. She was fond of diving into my pockets and extracting articles therefrom and then scampering away with them. She appeared to take a certain pleasure in being pursued for the recovery of the stolen property. Most things which she took went straight to her mouth. She was especially fond of chewing up lead pencils, and took an apparent delight in breaking things or pulling them to pieces. After a detailed investigation of an object for some minutes, during which she turned it over and over with her hands and feet—for she was almost as facile in grasping things with her feet as with her hands—she usually wearied of her plaything and gave it little further attention. This sort of intellectual curiosity afforded her many things with which to occupy herself; and when no other object engaged her attention she would frequently busy herself with inspecting her own person in the pursuit of possible parasites.

One marked trait of Lizzie's behavior was the ease with which she became alarmed at any unusual object or occurrence. After some months of acquaintance, when she would sit contentedly on my shoulder, any quick movement would inspire her with fear. A certain instinctive dread of being taken unawares seemed to be an ineradicable part of her mental make-up. Bred to a life of continued watchfulness and fear in the forests of her native home, she was gifted, to a very unusual degree, with the faculties that make for the ready detection and avoidance of danger. For keenness of perception, rapidity of action, facility in forming good practical judgments about ways and means of escaping pursuit and of attaining various other ends, Lizzie had few rivals in the animal world. She frequently surprised me by getting out at a half-opened door which I thought I had effectually guarded, or in grabbing a bit of food from me which I was confident she could not reach. Her perceptions and decisions were so much more rapid than my own that she would frequently transfer her attention, decide upon a line of action, and carry it into effect, before I was aware of what she was about. Until I came to guard against her nimble and unexpected maneuvers she succeeded in getting possession of many apples and peanuts which I had not intended to give her except upon the successful performance of some task.

In disposition Lizzie was gentle and tractable, and did not make more than a rather playful pretense of biting one's hand. Of affection or attachment to any one, such as has been described in other kinds of monkeys, Lizzie showed scarcely a trace. She seemed to enjoy the presence of people much as she would be gratified in examining a new kind of object; the pleasure she derived was an intellectual one rather than an emotional satisfaction such as a dog takes in his master. When she was irritated, which was easily done, she would give a sort of bark and face one with an open mouth and general attitude of attack. Fits of temper wore off very quickly, for she was very changeable in her moods as well as in her mental pursuits. She was also quickly over her fears. With her, sufficient not only for the day but for the moment was the evil thereof. She wasted no time in retrospection; she lived entirely in the present, and in one of very narrow span.

While Lizzie was a most admirably efficient little mechanism for getting on in life under the conditions of a tropical forest, she proved to be quite stupid when tested according to certain other standards. In order to get a clearer insight into her mentality, recourse was had to a number of experimental tests. The front of Lizzie's cage was made of vertical bars which were far enough apart to allow her to reach out her arm between them. A board was placed just outside her cage and a piece of apple put on the board beyond her reach. Lizzie grabbed at the apple, pushing the board to one side.

Then she tried to seize the board by one end and pull it toward her, but as the board was a little too heavy for her to move well in this manner, a nail was driven in the middle of the end of the board nearest the cage to serve as a sort of handle. When

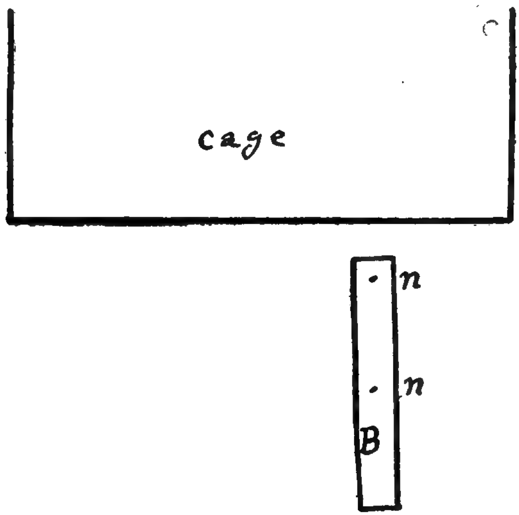


FIG. 11.—Diagram of Lizzie's cage with the board B, on which food was placed. n n, position of nails.

board and apple were placed as before Lizzie reached immediately for the nail, pulled the board in and got the apple. A repetition of the same experiment was followed at once by the same result. During the third trial Lizzie attempted to seize the board by the side and pushed it away out of reach. When the board was replaced she pulled it by the nail and got the apple, as she did also at the next trial.

In these experiments, even at first, Lizzie did not reach for the apple directly. She seemed to appreciate from her inspection of the situation that the apple could not be secured in this way. Her first efforts were directed to the means of attaining the desired end, and when the nail was driven into the board she seemed to apprehend at once how it could serve her purpose. There was no employment of the method of trial and error; there was direct appropriate action following the perception of her relation to board, nail and apple.

After the fourth trial, when the board was in its usual position and before the apple was on it, Lizzie reached out and pulled it in. In the fifth trial, when the apple was replaced, she seized the board by the side and pulled it in after considerable effort and got the food. Then the board was replaced with no apple on it, but it was pulled in again in apparent expectation of the usual reward. This futile performance was repeated several times. Finally Lizzie grew weary of her wasted efforts and would no longer respond. Then a piece of apple was placed about six inches to one side of the board. After making an ineffectual attempt to reach the apple directly, Lizzie seized the board and pulled it in. She did this six times, after which she sat looking at the apple and whining. Then I placed the apple on the board, which was immediately pulled in by the nail. After her appetite was whetted another piece of apple was placed six inches to one side of the board as before. Lizzie expectantly pulled the board in and repeated the performance six more times, but her actions became slower with each disappointment, until after the sixth trial she gave the board up and tried to reach the apple directly. Then I held the apple near the cage to give her a smell of it and replaced it near the board. Being thus stimulated, Lizzie pulled the board in by the nail three times, when she gave up the task. After being tempted as before she pulled the empty board in three times.

In these experiments Lizzie showed that she had associated the act of pulling in the board by the nail with obtaining and enjoying the apple. But her persistence in pulling in the board when she could clearly see that the apple was several inches away from it showed that she exercised little discrimination, and indicated that the associations she had formed were of a rather vague and hazy kind.

In another experiment I placed the apple further out on the same board so that she would be unable to reach the food when the near end of the board was against the base of her cage. Lizzie pulled the board in at once and reached for the apple. Finding it too far out, she pushed the end of the board sidewise, at the same time keeping it against the base of the cage. This brought the apple nearer and she got it. The experiment was repeated several times and Lizzie solved her problem each time with little or no hesitation, as in the first trial.

The problem was then made a little more difficult by placing the apple still farther out on the board so that she could not reach it even when she had pushed the end of the board as far to one side as the limits of her cage would permit. When she had pulled the board in and to one side, finding that the apple was still out of reach, she tried to seize the board by the side and to pull it in sidewise. It was too difficult for her to get a good hold of the board in this way, and her attempts were not successful. I then drove a nail near the middle of the board. Getting the apple involved pulling the board to the cage by the first nail, pushing it then to one side so as to bring the second nail within reach, seizing the board by the second nail and pulling it sidewise toward the cage until the apple was sufficiently near. At her first trial Lizzie pulled the board in by the first nail, then pulled it sidewise, and tried to seize the edge of the board. Apparently by accident her hand struck the second nail, which she seized at once, and by its means pulled in the board and got the apple. In the second trial Lizzie pulled the board in and to the left, then reached immediately for the second nail and pulled in the board toward her cage. In several subsequent trials she secured the apple in just the same way. The problem was solved perfectly after the first trial.

In another set of experiments Lizzie was given a vaseline bottle containing a peanut and closed with a cork. In accordance with her instinct to bite at new objects Lizzie attacked the cork with her teeth, pulled it out and tried to chew it, holding the bottle meanwhile in one hand; then she noticed the nut when she transferred the cork to her feet, and tried to reach the nut, but the neck of the bottle was too small for her hand to enter. On turning the bottle over the nut dropped out unobserved and I replaced it and put in the cork. Lizzie immediately drew the cork and held it in her hind feet while she tried to reach the nut with her fingers. Finally, when she was holding the bottle upside down, the nut came within reach of her fingers and she got it out. When given another nut in a corked bottle she pulled the cork and tried to reach the nut with the bottle upright, but in the course of her efforts she turned the bottle over so that the nut fell down within reach, when she got it.

Without describing in detail her subsequent trials, I may say that Lizzie gradually came in the course of fifteen trials to turn up the bottle very soon after she received it and to get the nut much more quickly than at first. She never came to turn the bottle over and let the nut drop out. She was too busy trying to reach it with her fingers to get it by the easiest method. Even after she had come to get the nut rather quickly she often spent considerable time in attempting to reach the nut when the bottle was held upright. She did not pick out the essential acts that led to success. She perceived that the nut could be secured by going through a certain series of motions, and the useless movements were gradually eliminated with an average shortening of the time necessary to gain the desired end. So far as her progress is concerned after she had removed the cork from the bottle, she gave no evidence of clearly perceiving how anything that she did furthered her purpose. Apparently she did not clearly apprehend that if she turned the bottle upside down the nut would fall down within reach of her fingers, although she had seen the nut fall dozens of times. In the course of her intent efforts her mind seemed so absorbed with the object of desire that it was never focussed on the means of attaining that object. There was no deliberation, and no discrimination between the important and the unimportant elements of her behavior. The gradually increasing facility of her performances depended on the apparently unconscious elimination of useless movements.

The previous experiments were modified by giving Lizzie a nut in a screw-cap Mason jar without a cover. She could easily reach into the wide mouth and get the nut, but she picked up the jar instead and turned it about. Having accidentally dropped the jar, she scuttled away in alarm, but she cautiously approached it again, turned it over and got the nut. Then she picked up the jar, carried it to her perch, rolling it over and over with her hands and feet in various ways. I took the jar and put another nut in it, but Lizzie continued to play with the jar and let the nut drop out unobserved. When the nut was replaced Lizzie tried to get it by biting the glass; in the course of her turning the bottle around, the nut dropped out and she picked it up. When another nut was put in Lizzie reached in at once and got it. Another nut was obtained in the same way, but at the next trial she turned the jar around in various ways until the nut fell out; and in numerous other trials on different days she sometimes got the nut by reaching it directly and at other times by turning the bottle around until the nut dropped out. Fifty or more trials did not teach her to secure the nut at once by inverting the bottle. While she came to get the nut by reaching into the jar more often than she did at first, she did not settle down to any uniform method of procedure.

When a nut was placed in the jar and the cover screwed on very loosely, Lizzie tried to pull the cover off by using her hands and teeth. After much effort she succeeded and held the jar with a hand and a foot and the cover with the other hand. The novelty of the cover engrossed her attention and she let the jar drop. Soon she went to the jar, reached in and got the nut, and then resumed her investigation of the cover.

Another nut was placed in the jar and the cover screwed on very loosely as before. Lizzie took the jar to her perch, worked the cover off with her hands and teeth, and then reached in and got the nut, holding the jar upright with her feet. The next trial resulted in practically the same way. The cap of the jar was then screwed on farther. Lizzie attacked the jar industriously and finally removed the cover, although working quite unsystematically. The cover was put on as before and Lizzie worked at it about fifteen minutes, getting more and more excited and impatient over her lack of success; sometimes she tried to bite through the glass at the lower edge. After turning the cover this way and that she finally unscrewed it and got the nut. After numerous trials Lizzie never learned to unscrew the cover by turning it around uniformly in one direction. She simply worked it back and forth until it happened to become entirely unscrewed.

Lizzie was then set to the task of getting food out of a small box. Two sides of the box were made of strong wire netting; the rest was wood. In one corner was a small door which could be fastened by a hook passing through a small screw eye. In the first experiments a piece of apple was placed in the box and the door, which stuck rather tightly, was left unhooked. Lizzie looked at me while I put the food through the door and she opened the door at once and got the food. She did the same at the second trial, after which, when the food was replaced, the box was turned so as to lie on another side. This seemed to disconcert Lizzie and she tried biting and clawing at the wire netting, and turning the box over and over until she became discouraged. I recalled her to the task by tapping on the box, but evoked only feeble efforts. When I opened and closed the door Lizzie observed me and went at once to the door and got the apple. Then I replaced the apple and closed the door and put the box in another position. Lizzie attacked the box in various places and then desisted. Soon she looked at the box, went to it as if an idea struck her, and tried to pull the door open by using hands and teeth; finally, after some tugging, she succeeded. After a few more successful trials the door was fastened with the hook. Lizzie attacked the door with hands and teeth and turned the box over and over and often tried to get the apple through the wire. A renewed attack on the hook enabled her to get the door open and get the apple. The next trial on the succeeding day was followed by much the same method of attack. After biting at the hinges and various other parts of the box Lizzie loosened the hook and opened the door.

Not to weary the reader with the recital of Lizzie's misdirected efforts and slow progress, it may be said that she gradually came to concentrate her efforts on the door, but even after thirty trials she would bite at the hinges and edges of the door, and not infrequently she would turn the box over and bite at the wire netting. In all of her efforts at the hook she never learned to pull it to one side. She simply tugged at it this way and that with her teeth until it came undone. The mechanism of the thing, *how* the hook stood in the way of opening the door, she could not understand, simple as it was.

When a button was substituted for the hook her mode of attack was much the same; and her progress, such as she made in the course of thirty trials, was after the same slow method. She never perceived that when the button was turned in one direction it left the door free to come open, and that it prevented the door from coming open when it was in another position. She bit and worried away at the button, and pulled at the door until she got it open and got her food. The idea of the thing never got into her head.

When both the hook and the button were used Lizzie had a very hard time to get her food. Occasionally after much varied and fruitless effort she would succeed. If she got the button turned right she would usually turn it the wrong way before she undid the hook. The experiments would probably have discouraged her observer had they not usually wearied their subject before she met with success. There was little hope that she would be able to solve more complex problems.

A peanut that was hung below her at the end of a cord she obtained by pulling up the cord, hand over hand, the very first time she saw it. I tried to teach her to use a stick to pull in food with, as monkeys have sometimes been described as doing, but met with no success. Placing a bit of food outside the cage, I poked it about with the stick so as to give her a suggestion of how the stick might be employed to move the food within reach, but although the act was repeated many times, Lizzie never showed the least inclination to use the stick to her advantage. In fact, she never exhibited the least tendency to use any object as a tool.

Next I tried suspending a piece of food beyond her reach and giving her a light box upon which she might mount and get the food. She did this readily enough when the box was in the right position. Then the box was pulled to one side in order to see if she would pull it back so that she could get upon it and reach the food. Although I frequently moved the box about to give her the suggestion and often put it in the proper place to enable her to get the food, the idea of using the box in the way described never seemed to occur to her.

Experiments with Lizzie were brought to a close by her death, but the results obtained were sufficient to give some insight into the nature and limitations of her mental endowments. While gifted with remarkably quick perception and in certain respects power of rapid judgment, nothing in her behavior gave any indication of the use of abstract or general ideas, or of deliberate reasoning. Neither did she exhibit the least tendency toward imitation, although I am not prepared to say that further experimentation might not have revealed some evidence of this faculty. Some things, and even simple things, she apparently learned by the primitive method of the gradual elimination of useless movements after attaining a chance success. This type of learning is the one mainly followed by the less-developed mammals, but in the apes the curve of learning simple things usually shows a sudden descent from the start. One reason for her comparatively slow progress in the experiments with the boxes and the bottles is, I suspect, that in her eagerness to attain the desired end her attention was never strongly directed to the means employed. When we attempt to solve a puzzle we direct our attention to the means we employ and pass judgments upon them, but Lizzie never discovered the value of paying attention to method. Her impulsiveness and activity stood in the way of her attaining any results that required a small amount of deliberation.

The perception of very simple relations usually escaped her. She never clearly perceived that a hook could be unfastened by simply pulling it to one side, that a button would not hold a door closed when turned in a certain position; she probably never became clearly aware that when a bottle was turned upside down its contents would fall out. As we know these things, they involve a certain prevision, or representation to ourselves of how certain things might happen if certain conditions were fulfilled. But this power was but slightly developed in Lizzie's mind. There are more indications of it in Lizzie's performances in pulling in the board by the two nails. The quickness with which she learned the elements of the trick indicated that she perceived the way in which it might be done by simply inspecting the situation. But we should be cautious in our interpretations, because it was not known how near such actions might have been to her previous experience. Had she, for instance, been used to pulling in branches with fruit attached to them, pulling in the board might have been a particular application of some of her previous activities for which she may have had a strong instinctive bent.

While it may not be safe to deny to Lizzie a certain amount of prevision in her performances with the board, we should hardly be justified in saying that they necessarily involved the drawing of an explicit inference. Should one ask if Lizzie were able to reason, the answer would have to depend on how reason were defined. That some of her acts are the outcome of simple inference, though perhaps not explicitly formulated in her mind, is quite probable. Even perception, as Spencer, Binet, and others have shown, is allied to inference; and Lizzie's behavior evinces a much closer approach to the rational type than does the process of simple perception. Her behavior does not indicate so high a degree of mental development as that of several other monkeys that have been the subject of experiment. Whether her relative ineptitude for certain tasks is an individual peculiarity or a trait characteristic of her species cannot be stated with any assurance.

As I have remarked in another work, "We are apt to overestimate the importance of the ability to reason as if it were the chief thing of value in intelligent behavior. There are other mental traits which may enable an animal to get what it wants better than an increment of reasoning power. General activity, power of attention, interest, quickness of forming associations, delicacy of discrimination, duration of memory, and the ability to form complex associations are all of the utmost importance in many situations of an animal's life. . . . Give a fox greater power of inferential thinking, but decrease his alertness, curiosity, suspiciousness, and quickness of perception, and he might fall a victim to the hunter while his mind was employed on some other subject." Possibly more intelligence of the human sort would have been a positive drawback under the conditions of Lizzie's natural environment.

INDEX

ARTI et VERITATI