spheric flares and flare-associated phenomena represent the most violent forms of solar activity and produce profound effects in our outer atmosphere and in our space environment.

Bursts of far-ultraviolet and x-radiation that produce ionospheric storms, great proton showers that bombard the polar regions of the earth, high-energy solar cosmic rays, and the lower-energy plasma clouds that result in geomagnetic storms and produce auroral displays are all strongly associated with flares. The immediate source of some of these irregular solar radiations is probably the corona surrounding the flare, or perhaps even the photosphere below the flare. Nevertheless, the chromosphere is intimately involved in the flare phenomenon.

The most intense emission lines and continua in the far-ultraviolet region of the solar spectrum, as observed by rockets and satellites, arise from chromospheric hydrogen, helium, and heavier elements in early stages of ionization. These radiations produce and control much of the terrestrial ionosphere and play an important role in the energy budget of the earth's outer atmosphere.

An understanding of the sun's atmosphere and of solar activity in its many forms is of great importance in all our space programs and in upper-atmosphere research. Strong additional interest is being generated by current emphasis on the production and study of high-energy plasmas in attempts to produce controlled nuclear fusion in the laboratory. Many of the phenomena observed in the laboratory have a marked resemblance to phenomena of the solar atmosphere. Thus, we now have, for the first time, the possibility of performing laboratory experiments in chromospheric and coronal physics. Similarly, plasma physicists are recognizing that the chromosphere and the corona are "laboratories" in which interesting experiments are continuously in progress. Interaction of the laboratory studies of plasma physics with studies of chromospheric and coronal physics will undoubtedly increase our understanding of this complex and interesting region of the solar atmosphere.

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Microscopic Brains

The behavior of insects and vertebrates may not differ qualitatively to the extent that had been supposed.

V. G. Dethier

The study of animal behavior is unique among the sciences because it begins historically and methodologically with human behavior, prescinds from human experience, and projects this experience into other animals. It is thus more disposed to subjectivity and introspection than the other sciences and constantly labors under the burden of containing these biases within the bounds of their historical context. The study of man himself is further complicated by the fact that the investigator is trying essentially to understand himself, and others through himself, and in so doing is employing a brain to understand a brain.

Students of behavior tend to seek in other animals that which they believe exists in themselves. They look for motivation, drive, emotion, perception, consciousness, ideation, mood, sensation, and learning. Common sense assures us that it would be absurd to deny the existence of these phenomena. Those to whom an appeal to common sense borders on scientific heresy need only peruse the *Handbook of Physiology* and dwell upon the chapter headings: "Drive and motivation," "Emotional behavior," "Attention, consciousness, sleep, and wakefulness," "Perception," "Thinking, imagery, and memory." These are real phenomena. Faced with defining them, however, we bog down in a morass of ignorance, confusion, anthropomorphism, and verbal gymnastics to escape anthropomorphism.

Given this background, how can one ever study these states outside the context of human behavior? Certainly the most obvious and tangible approach is a search for physiological correlates. When a dog which is teased by a stranger bares its fangs, raises its hackles, snarls, and lunges, we say that it is enraged. Whether it is or not we shall probably never know, any more than we can ever know when a fellow human is enraged. On the other hand, we can ask meaningful and testable physiological questions about the dog's behavior in this situation, which so closely mimics our own emotion in comparable situations. We can investigate the conditions under which hair is erected, adrenalin is secreted, teeth are bared. It may even be possible to gain some insight into possible affective components of this behavior through employment of the self-stimulation techniques discovered by Olds and Milner (*1*).

Viewed in this light, it is clear that higher animals, mammals especially, exhibit a rich repertoire of behavior comprehended under the terms motivational, emotional, and so on which seems to be absent to varying degrees in the so-called lower animals. The farther removed an animal is from ourselves, the less sympathetic we are in ascribing to it those components of behavior that we know in ourselves.

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There is some fuzzy point of transition in the phylogenetic scale where our empathizing acquires an unsavory aura. Yet there is little justification for this schism. If we subscribe to the idea of a lineal evolution of behavior, there is no reason for failing to search for adumbrations of higher behavior in invertebrates. If, on the other hand, we believe in a behavioral dichotomy, in the idea that the invertebrates differ qualitatively from the vertebrates, it behooves us to put the belief to test.

In the latter part of the 19th century and the first quarter of the present one, students of behavior, especially of insect behavior, identified themselves so thoroughly with their subjects that their observations led to uncritical anecdotal interpretations (see *2*). The reaction that followed is epitomized in the words of Schneirla (*3*): "Anthropomorphism is a doubtful practice for scientists interested in understanding the real nature of behavior." Yet without a disciplined anthropomorphism inquiry into behavior is hobbled. Anthropomorphism has an heuristic value at this stage of inquiry and should be exploited with more courage.

Consider for example the insects, whose patterns of behavior are so complex and humanly mimetic that they have been held up for emulation since Solomon's time. It is considered unforgivable for scientists to speak of the rage, aggression, awareness, sensation, drive, and wakefulness of insects. Only the poet is permitted to speak the phrase "mad as a hornet." Insects are said to be stimulus-bound and instinctively fixed—little machines in a deep sleep—which implies, of course, that higher animals are not. This juxtaposition raises some profoundly interesting questions: Do insects indeed lack higher categories of behavior or is it that being anatomically different from us they do not show, for example, emotion because their eyes are pupilless and immobile, because they do not cry, sweat, or sulk? Or is it that experimentalists do not ask these questions of insects, and hence by default have assigned them a behaviorally inferior role? Or is it that, truly lacking this behavior, insects show a deficit because their nervous system is handicapped by having fewer cells in its minute mass? Or is there perhaps a qualitative (recognizing, of course, that a sufficient number of quantitative differences constitute a qualitative one) difference between the mammalian and the insect nervous systems? And if the answers to the last two questions be in the affirmative, how does the conclusion affect our concepts of the evolution of animal behavior and of behavior in general?

The proper approach to this problem is one for pondering. Neurological analyses of behavior have proceeded for a long time on the assumption that unit analysis will yield the answers. There is a growing feeling in some quarters, however, that the key to understanding lies in other parameters of neuronal systems, a view espoused particularly by Bullock (*4*). Physiologists studying behavior believe in any case that the ultimate solutions lie in a clearer understanding of sensory and synaptic events and nerve impulse transmission (for example, *5*, *6*). A number of psychologists, on the other hand, believe that the complexity of events controlling behavior is too great to be analyzed in these terms and that large-scale psychological concepts must be used in conjunction with the smaller-scale neurological ones (*7*). Guttman in a provocative essay on "Laws of behavior and facts of perception" proposes (*8*) a methodological dualism for studying perception (sensation, sensory integration, and perception) on the one hand and what the animal "does" on the other. Gregory maintains (*9*) that behavior should be analyzed as the output of a machine. The sentiments of the psychologists emphasize the reality of the questions I posed earlier, while the attitude of the cyberneticists, who would treat animals as machines, suggests that the questions might best be answered by experiments with simple organisms.

Motivation

Let us approach these problems by selecting what appears on the surface to be one of the more simple concepts and one most amenable to analysis—namely, the concept of motivation. And let us search for evidence of motivated behavior in the fly, as much for insight into the methods of analysis and for testing the applicability of the concept of motivation to *all* animals as for arriving at a definitive answer to the question of its existence in insects.

But first, what is motivation? This may be a brash question indeed. Most people, however, seem to have an intuitive idea what motivation is, although they either hesitate to commit themselves verbally or find the idea too elusive to state. Let us attempt to formulate a statement. Motivation is a specific state of endogenous activity in the brain which, under the modifying influence of internal conditions and sensory input, leads to behavior resulting in sensory feedback or change in internal milieu, which then causes a change (reduction, inhibition, or another) in the initial endogenous activity. The essence of motivation is endogenous activity, in the brain, correlated with a particular kind of behavior. The level of motivation can be inferred by the amount of work (frequency, speed, quantity, general activity, and so on) an animal will perform in order to carry out the specific behavior or by the intensity of adverse stimulation (for example, shock) that an animal will tolerate to the same end. This measure (drive) is not an infallible assessment of motivation because many other patterns of behavior exhibit orderly changes in activity associated with deprivation. The most unequivocal measure may be operant conditioning, as Teitlebaum has suggested (*10*), because the operant is essentially a voluntary act, not dependent upon specific afferent input, that an animal can use to obtain reinforcement. Since the animal exerts control over the occurrence of its response, the behavior is distinct from reflexes and from complex fixed motor patterns. Demonstration of an endogenous center by electrical recording therefrom or by eliciting patterned behavior by local brain stimulation is not alone convincing evidence for motivation. Nor is the occurrence of vacuum activity—that is, spontaneous response during deprivation in the absence of specific stimulation. On the other hand, if the behavior in question cannot be manipulated operantly, this of itself is no indication of lack of motivation because the animal may be a "nonlearner." One might argue that if learning is a criterion for motivation and an animal cannot learn, then it cannot be motivated. Here, however, learning is proposed as a criterion for detecting motivation and not as a *sine qua non* for its existence. Conceivably an animal could be capable of exerting voluntary control over its behavior without exhibiting a demonstrable capacity for learning. One need not look far beyond our own species for examples.

Objections to this definition of motivation may be raised on the grounds that it is too restrictive and that it places a well-recognized category of behavior into a hypothetical and experimentally inaccessible area of the nervous system. On the other hand, the usual operational descriptions of motivated behavior may be so broad and undiscriminating as to construe all behavior as motivated. If, for example, motivated behavior is described simply as goal-directed behavior with a drive component (change in activity), then the phototactic behavior of a moth could conceivably be construed as motivated, the light being the goal, compulsive flight representing the drive component, and the moth coming to rest in the vicinity of the light representing drive reduction. Similarly, the chemotactic responses of male moths to the sex attractants of the female would also come under the category of motivated behavior because the female would be the goal, flight would be the drive component, and the cessation of flight and failure to fly again after contact with the female would represent drive reduction. Even more broad is the designation of all random, unoriented, restless behavior, the appetitive behavior of Lorenz, as the outward manifestation of a mounting internal drive. It would seem that definitions so broad as to encompass within their bounds at one and the same time tactic behavior and such acknowledged motivated behavior as feeding by the rat invite an informational loss and raise the danger of obscuring meaningful differences of a fundamental nature. It is hoped that the point of being able to distinguish in a given behavioral situation between the kind of mechanism that fits the restricted definition given initially and alternate kinds of mechanisms will become clear in the following examples.

Hunger in the Fly

Let us commence by selecting and analyzing in detail one of the more intensively studied kinds of behavior—namely, feeding behavior, or in the context of our questions, hunger and satiation. In ourselves, hunger is a state defined by absence of food and feeding. A number of sensations—fullness or hunger pangs, as the case may be, euphoria, distress, and others—are associated with hunger; that is, hunger has an affective component. It leads to highly motivated behavior. It has a drive component; hungry men and animals will learn to work hard for food and will tolerate high levels of aversive stimuli. Does this picture accurately represent the state of affairs in insects or are there fundamental differences? Is the insect merely a pushbutton machine whose behavior is satisfactorily explained in stimulus-response terms or is there more to the picture? Is it useful to investigate hunger and satiation instead of restricting inquiry to the regulation of feeding?

The normal pattern of feeding in the blowfly is as follows (*11*). The fly moves about actively and randomly, flying or walking. If odorous food is available, the fly orients to it by means of information received through olfactory receptors on the antennae and palpi (*12*). Upon encountering the food the fly steps in it, thus stimulating taste receptors on the tarsi. These receptors trigger extension of the retractable proboscis, bringing marginal labellar taste hairs into contact with the solution. As these hairs are stimulated the labellar lobes are spread, bringing another set of taste receptors, the interpseudotracheal papillae, in touch with the solution. Sucking commences, food is swallowed, and at the conclusion of a meal some regurgitation occurs.

Feeding is thus under the control of four sets of sense organs: antennal and palpal olfactory organs, tarsal taste receptors, marginal labellar taste hairs, and interpseudotracheal taste papillae. Each locus contains receptors mediating acceptance and receptors mediating rejection. Feeding is monitored at each level and can be terminated if rejection receptors are stimulated or if acceptance receptors become adapted.

For any given state of the fly there are two stimulus variables influencing feeding activity: kind of sugar and concentration. These affect threshold of acceptance, speed of sucking, and duration of sucking. It is important to note that the order of effectiveness of sugars bears no relation to metabolic value. (*13*). Thresholds, therefore, reflect stimulating effectiveness. All acceptable sugars can have the same effect behaviorally (for example, they may cause meals of equal volume to be taken) if concentrations are matched, as seen in preference tests. For any given sugar, the speed and duration of sucking depend solely on concentration unless an impeding factor such as viscosity begins to operate. The rate of sensory adaptation also varies as a function of concentration. It is through this mechanism that the duration of sucking is controlled.

The short-term pattern of feeding is determined by these factors and by postingestion factors. Feeding is largely driven by sensory input. As food is sucked into the esophagus by the pharyngeal pump, peristalsis originating in the esophagus drives the food first directly into the mid-gut, then into the crop, a blind diverticulum which serves as a storage reservoir. After intake is terminated (by sensory adaptation), antiperistalsis in the crop duct periodically returns slugs of food to the esophagus, whence peristalsis now drives it into the mid-gut, the crop valve having closed, the mid-gut valve being open. From the mid-gut food is absorbed into the blood, whence it is mobilized in the glycogen of the muscles and the fat body. There are thus four energy storage depots: crop, blood, glycogen, and fat body.

Thus a "meal" for the fly may be described as follows. Volumetric intake is under the control of the sensory input. When sensory adaptation occurs, feeding stops but may resume intermittently over the next few minutes as disadaptation and adaptation fluctuate. Soon, however, the meal terminates. Now the fly cannot be induced to feed further. At this juncture postingestion factors inhibit feeding, and the duration and time course of their operation depend upon the concentration and volume of sugar ingested. During this refractory period a number of physiological changes have been measured: rate of crop emptying, change in gut contents and motility, change in blood-sugar level, and changes in threshold (*14*). The rate at which the crop empties by transferring solution to the mid-gut is at first rapid, then decreases slowly. At the same time the level of sugar in the blood increases shortly after feeding, then falls rapidly as the crop becomes empty. Coincident with these events the acceptance threshold, that is, the concentration of sugar required to reinitiate feeding, falls. In a series of operations involving ligaturing full and empty crops and mid-gut, loading the mid-gut by enema, injecting sugar into the blood, and making parabiotic twins of fed and hungry flies, Bodenstein and I showed (*15*) that the acceptance threshold remained unchanged. Transection of the recurrent nerve, however, that section of the stomatogastric nervous system supplying the alimentary canal, caused flies to become hyperphagic. In other words, the mechanism for shutting off ingestion no longer functioned normally. Bodenstein and I postulated that the recurrent nerve carries back to the brain inhibitory impulses which originate in receptors in the esophagus stimulated by the periodic regurgitation from the crop as it transfers fluid to the mid-gut. We suggested that the inhibitory feedback nullifies input from the oral taste organs, this being reflected as a rise in acceptance threshold. Reexamining the question, Evans and Barton Browne concluded (*16*) that the mechanism did not involve a rise in sugar threshold but did involve a change in responsiveness to water (in which all sugar was presented). In any case, events monitored in the esophageal region normally inhibit further intake.

Locomotor Activity

There is still another behavioral event correlated with deprivation, general bodily activity. When a fly is allowed to spend its entire life in a minute actograph under normal lighting conditions but without food, it exhibits a prounounced circadial activity rhythm. This rhythm persists in total darkness and can be reversed. In constant light, however, it is more or less completely damped. Under these conditions an emerging fly is quiescent, except for occasional short bursts of activity during the first 72 hours of life. At 72 hours activity begins in earnest, increases to a maximum at 84 to 96 hours, then begins to wane, foreshadowing death. If the fly is fed during its period of activity, movement drops to zero. The time required to attain once again the initial rate depends on the concentration and volume of ingested sugar.

Thus there are two overt behavioral manifestations of deprivation, increased activity and lowered acceptance threshold. It is possible to explain all of the feeding behavior of the fly in terms of these two variables. The lifetime feeding behavior of a fly and the behavior of a fly in a two-choice situation will illustrate this point. At the time of emergence from the pupal state the fly has completed all growth and cell division (gonads excepted) and can live out its full life span (about 60 days) on a diet of pure carbohydrate. Immediately upon emergence it takes very little 0.1-molar sucrose (a concentration insuring maximum longevity) but rapidly increases its consumption to a maximum by the 2nd or 3rd day. From then on intake is fairly constant except for minor fluctuations due to differences in activity. There may be a gradual decline with age; there is a precipitous decline before death.

With a more concentrated sugar—for example 1.0 molar sucrose—the overall pattern is similar but the volume intake is markedly increased during the first four days, and thereafter is considerably less than it is for 0.1-molar sugar. When the fly is presented alternately with "high" and "low" sugar at 48-hour periods, the volume of "low" sugar taken is always less than the volume of "high." Thus it might be said that the fly regulates its caloric intake. Since 0.1-molar sugar provided maximum longevity and since the volume of 1.0-molar, even though reduced, provided an excess of sugar, it would seem that the regulation is not absolute. The change in intake can be explained fully in terms of changes in activity and the dependence of rate of sucking, rate of adaptation and disadaptation, and rate of crop emptying upon the concentration of sugar encountered (*17*). In a two-choice situation the fly always imbibes a greater volume of the more stimulating of the two solutions, whether it be a higher concentration of the same sugar or an intrinsically more stimulating one. In this situation a fly always takes a highly stimulating non-nutritive sugar in preference to a poorly stimulating nutritive one.

Thus the feeding behavior of the fly in choice situations and in deprivation and satiation can be adequately explained in stimulus-response terms. Is this the whole story? We now return to our primary questions. Clearly there are differences between a fed and an unfed fly, but is the unfed fly "hungry" and do we gain by asking if it is hungry? Is feeding behavior motivated behavior?

Measures of Motivation in the Fly

At the simplest level of inquiry one searches for a drive component. Is there a positive correlation between the general bodily activity of the fly and its state of deprivation? Clearly the answer is yes. As Green has shown (*18*), however, the fly does not move faster; it merely moves more often. Will a hungry fly suck faster or eat longer than a satiated fly? Clearly, for a given concentration, the answer is yes. But this, at least hypothetically, is explainable in terms of interaction between a standard sensory input and a variable inhibitory feedback via the recurrent nerve. Will the fly work harder to obtain food? Here the anser is in doubt. A number of laboratories, our own included, have attempted over the last decade to induce a fly to press a bar for food or to run a maze. So far these attempts have met with consistent failure. Bar-pressing devices that flies can operate have been built, but the animals have never cooperated—possibly because the situation is too foreign to their natural history. Attempts have also been made to detect an increase in flying effort as measured by frequency of wing-beat when a deprived fly is exposed to the odor of food (*19*). In this case the fly was *Drosophila* and the food, bananas. A deprived fly did not fly any more vigorously than a satiated fly. In this connection it is of interest that hungry flies are more "persistent" in their efforts to come to food (as are hungry mosquitoes) and can be discouraged only with great effort, but this behavior is explainable on the basis of increased general activity with deprivation.

No attempts have yet been made to measure the amount of electric shock a fly will tolerate in order to obtain food, and this measure might be informative. Measurements have been made of the amount of adversely stimulating adulterants a fly will tolerate in its food as it gets hungrier, but the data cannot be interpreted as usefully as we would like. At first glance it appears that a hungry fly does indeed tolerate more salt than a fed fly, but this finding is deceptive. Feeding represents a favorable balance between acceptable and unacceptable sensory input. For example, if a small amount of salt is added to sugar, imbibition continues unabated; if more salt is added, sucking stops. Now if the sugar concentration is increased, intake resumes even though the high concentration of salt remains. In other words, the sensory input from sugar receptors must exceed the input from salt receptors if feeding is to result. It has been pointed out, however, that the sugar threshold drops with deprivation. That is to say, fewer sugar impulses are required to trigger the event, so when a deprived fly tolerates more salt in a standard sugar solution it means simply that the lower threshold to sugar is, in effect, an increase in sugar concentration; so the net result is a sugar-salt balance in the central nervous system still in favor of the sugar. It would be highly instructive to reapply the test of salt tolerance by adjusting the sugar concentration with each stage of deprivation to a threshold criterion. A few experiments of this sort were conducted by Haslinger (*20*) with a related fly, *Calliphora erythrocephala*. The rejection threshold for hydrochloric acid during starvation was measured by presenting the acid in a fructose solution, the concentration of which was varied so as to be just 3 times the threshold for fructose on each day of the test. Under these conditions no change in the rejection threshold for acid was observed. Similar results were obtained with unacceptable sugar alcohols, salts, and quinine. In other words, the insect did not tolerate more adversity. On the other hand, the efficacy of skin repellents against mosquitoes is an example of an adverse stimulus whose effectiveness clearly varies with the state of deprivation of the insect.

Endogenous Activity

Increased general activity correlated with deprivation can be analyzed through additional steps. The analysis introduces the concept of endogenous activity in the central nervous system. As Roeder (*5, 21*) has pointed out, reflex physiology with its assumption of neurological silence in the absence of overt stimulation has failed to provide a basis for explaining behavior even in insects. Endogenous activity in receptor and central neurons is widespread among invertebrates, having been first detected by Adrian in caterpillars (*22*). Its characteristics and neuronal bases have been discussed most recently by Kennedy, Van der Kloot, and Bullock (*23, 24*). In general, insects have spontaneously active motor centers in the subesophageal ganglion through which stimuli act to excite thoracic locomotor centers. In the supraesophageal ganglion there are centers which inhibit the activity centers (*25*). Recently Huber (*26*) has shown by local brain lesions and point stimulation in the cricket that there are two centers in the brain concerned with locomotion, one in the corpora pedunculata which inhibits the subesophageal ganglion and one in the corpus centrale which excites the subesophageal ganglion. The subesophageal ganglion regulates the degree of excitation of the thoracic ganglion. Thus the head determines the onset and duration of locomotion and, in conjunction with head sensory input, the direction. The thoracic ganglion together with proprioceptive input from the legs actually promotes locomotion.

Ethologists have long contended that appetitive behavior (drive) derives from an endogenous activity reasonably supposed to be a manifestation of endogenous nerve activity. As Roeder (*21*) has pointed out, it is not easy to devise experiments that will demonstrate a connection between appetitive behavior and endogenous neural activity. He and his co-workers (*27*) demonstrated that copulatory movements by the praying mantis are endogenous in origin and that both copulatory movements and endogenous activity of motor neurons supplying the abdominal appendages are under the inhibitory control of the subesophageal ganglion. Spontaneous activity in abdominal ganglia increases markedly when the ganglia are completely isolated from the rest of the nervous system (*27, 28*).

No such neat correlation has been demonstrated with the fly; it is more than likely, however, that a correlation exists. Unpublished experiments from our laboratory show that the fly is like other insects in that removal of the subesophageal ganglion results in akinesis. This finding suggests the presence of an excitatory locomotor center. The animal can still walk briefly in a coordinated fashion if strongly stimulated; hence the thoracic center by itself can pattern walking. Removal of the supraesophageal ganglion promotes continuous locomotion. It has been shown, furthermore, that the following factors do not affect locomotor activity: increase in weight after a meal, metabolic state (that is, nutritional state), blood sugar concentration, blood potassium level (*16*), age, stretch receptors in the abdomen or the crop or posterior portions of its duct, limitations on oxygen reaching the thorax and legs from the abdominal air sacs, or constant stimulation of oral receptors during regurgitation (*18*). Green (*18*) has suggested that spontaneous locomotor activity in the fly is affected by a hormonal factor derived from the neurosecretory cells of the brain or the corpus cardiacum, or both.

Role of Hormones

Evidence to the effect that there are indeed hormonal changes associated with changes in general activity and with feeding has been obtained with other species of insects. Harker (*29*) has reported, for example, that endocrine secretions from the subesophageal ganglion, and probably the corpora allata also, may be involved in circadian activity rhythms. In locusts starvation increases spontaneous locomotor activity (*30*), speed of movement, and time spent in marching (*31*). When a locust has fed, the titer of potassium ions in the blood increases. It decreases with deprivation. For any given motor nerve output a starved locust (low potassium) responds with greater muscular activity than a satiated (high potassium) locust (*32*). A satiated hopper will still march, but the sensory input required to initiate locomotion must be greater. Hormonal changes are also involved. Ecdysone, the hormone of the prothoracic gland, is involved in processes which lead to differential effects on activity of the central nervous system and motor nervous system. It increases electrical activity in the cord and decreases it in metathoracic motor nerves (*33*). Haskell and Moorhouse (*33*) have postulated that the utilization of information by the centers depends on the influence of hormonal balance on integrative and other centers. That there are causal relations among feeding, hormone balance, and spontaneous activity in the central nervous system is almost certain. As early as 1934 Wigglesworth (*34*) showed that after the bug *Rhodnius* has had a blood meal, the swelling of the abdomen sends messages via the ventral nerve cord to the brain whereupon the medial neurosecretory cells secrete a hormone which is eventually released by the corpora cardiaca to trigger a moult. Later Van der Kloot (*35*) found that impulses would be recorded from the nervus cardiacium I when the abdomen was stretched, but only then. Feeding by a cockroach causes neurosecretory cells in the protocerebrum to become active (*36*) and the corpora cardiaca to release a pharmacologically active substance into the blood (*37*). The release of hormones at feeding is triggered by receptors in the labrum (*38*). The secreted material causes an increase (13 to 21 percent) in heart rate over its initial value (*38*). A hyperglycemic factor has been found in the corpus cardiacum (*39*). The corpora cardiaca also release active materials when animals are exposed to stress (for example, electrical stimulation, surgery, handling) (*40*). Extracts of corpus allatum depress spontaneous activity in the isolated nerve cord (*41*), while extracts from the corpora cardiaca inhibit impulses from the inhibitory center in the subesophageal ganglion and impulses impinging on efferent nerve cells in cercal and metathoracic ganglia (*42*).

All of these data, though fragmentary and derived from a number of species, support the general picture of a behavioral activity arising from spontaneous activity in the central nervous system and modified at feeding through the mediation of substances released into the blood by the endocrine system in such a manner that the modulating influence of sensory input on endogenous activity is altered.

This picture, however, does not differentiate fixed pattern behavior from the motivational behavior of our definition. It merely says that there are fixed patterns of behavior whose expression depends on endogenous neural activity modified by the internal environment and thus indirectly or directly by sensory input from the outside.

Fixed Patterns in the Brain

Extensive neurophysiological analyses have begun to reveal something of the neural mechanisms concerned in the execution of these patterns. The classical techniques of gross ablation (reviewed by Ten Cate, *43*) have been replaced by the more precise techniques of local lesions and local stimulation (*26, 44–49*). According to Huber (*45*) these analyses reveal, in the cricket, two categories of behavior: (i) movement patterns in which the interplay of effectors can be modulated by different input from the periphery (for example, walking, copulation, egg-laying); (ii) movement patterns which are almost irrevocably set by the central nervous system (for example, grooming, singing, flying). Local stimulation of the brain elicits from specific points ordered and coordinated patterns. At any point, however, there are changes in latency, threshold, and activation (from activation to inhibition). In some cases (for example, acoustic behavior) where action depends on momentary endogenous states there are changes in threshold related to these. In other cases (for example, copulation and oviposition) only the first local stimulation is effective because a certain constellation of stimuli from the periphery is required. The behavior pattern evoked may be very complex and its various phases may come into action sequentially, depending on the order of their respective thresholds. For example, local stimulation in the cricket may produce the following actions, in this order: increase in respiration, antennal and head movements, walking, jumping.

These analyses have shown, furthermore, that such a seemingly simple action as walking is in reality part of complex behavioral situations. As Huber (*26*) has shown, one category of behavioral situation of which walking is an element is flight, hole inspection, and attack. Walking is also an element of food searching, burrow construction, courting, and postmating behavior. Brain stimulation in some animals caused locomotion coupled with orienting movements of the antennae and palpi, and feeding when food was encountered. A change in threshold with satiation was noted. Huber believes that the searching movements, together with the taking of food, support the hypothesis that activation of an eating drive has occurred.

A demonstration of "little motors" which can be stimulated electrically hardly confirms the idea of motivation. I am inclined to agree with Teitlebaum that there must be an element of arbitrariness in motivation to distinguish it from complex fixed motor patterns and that this can best be sought by seeking a behavior that builds up in the absence of stimulation, with some state of deprivation, has a drive component, is goal-directed and satiates, can then be correlated with endogenous activity in the central nervous system, and can be operantly conditioned. The endogenous element separates it from reflex systems; the element of operant manipulation separates it from fixed motor patterns.

The failure to be able to manipulate a fly operantly is indeed a stumbling block to applying the crucial test to its feeding behavior. In the absence of this test the behavior can be explained adequately in terms of stimulus-response combined with fixed patterns. The fly can still be a little machine—true, not a push-button one, but nonetheless a rigidly programmed one and to this extent different from the mammal.

At this point, until some success attends efforts to demonstrate operant conditioning, the analysis should probably be transferred to an insect whose learning ability is indisputable. The honey bee is an admirable example of a learner. Unfortunately there is not the wealth of physiological information that exists for the fly and the cockroach. One fact is important, however: the honey bee can be trained to come to a feeding place at a specific time for food (*50*). This finding suggests that bees are motivated in that they have "voluntary" control over a fixed pattern. The bee cannot be made to go for food at an hour (for example, 9 P.M.) when she does not normally fly, but she can be made to suppress her flying activity during the normal hours of flying except at the appointed hour and then to show appetitive behavior in advance of specific stimulation. She can be trained to go to different places (as many as five) at different times and will continue to do so without reinforcement for as long as 6 days. This behavior meets our specifications for motivated behavior.

If motivated behavior can be shown in a learner such as the honey bee, it is not unreasonable to suspect that it is also characteristic of species with similar brains even though these species may not be capable of operant conditioning. All these things considered, therefore, it does not seem improbable that insects are capable of motivated behavior even in the restricted context of our definition. This being the case, motivated behavior is not confined to the higher vertebrates and, at least insofar as this aspect of higher behavior is concerned, one need not propose a dichotomy of function. Furthermore, since the insect brain is obviously smaller and less complex, perhaps we must revise our estimates of the minimum requirements for certain kinds of behavior, because it follows that at least the potential for some kinds of learning and for motivation does not have a prerequisite of large mass, cell numbers, and complexity.

The Insect Brain

The foregoing conclusion drives us to look at the small insect brain from a new perspective and with less stultifying preconceptions. The brain of a blowfly weighs about 0.84 milligram (wet weight). Its maximum linear dimension is 1583 microns. It probably contains not more than 100,000 cells. The smallest brains of equal complexity in any insect with equally rich behavior are the brain of the culicoid midge or no-see-um and the brain of the African ant *Oligomyrmex*. The former is 200 microns in its greatest dimensions; the latter, 150 microns. In each case the brain consists of a central feltwork of nerve processes, the neuropile, interspersed with fiber tracts, the whole overlain cortically with the cell bodies. This neural mass is encased in a sheath of non-neural connective tissue cells or glial elements. The most striking organizational feature of the insect brain is the sharp separation of cell body regions and synaptic fields. In contrast to the vertebrate brain, where cell bodies may lie in intimate association with dendrite fields, most of the cell bodies of the insect brain lie far removed at the periphery.

At the next level of structural organization the brain consists of three divisions; protocerebrum, deutocerebrum, and tritocerebrum. In the protocerebrum there are three systems of association neurons: the paired corpora pedunculata (mushroom bodies), the corpus centrale, and the horse-shoe-shaped pons. The fibers of these systems do not leave the brain. Instead they form synaptic connections with afferent and efferent fibers from all parts. The protocerebrum also receives the afferent tracts from the eyes. Antennal tracts enter the deutocerebrum. The tritocerebrum connects with the visceral system.

The greatest mass of the brain (33 to 80 percent) is made up of the paired optic lobes (*51*). Next in order of size (2 to 40 percent) are the mushroom bodies, between which lies the small central body. There are also small paired antennal centers (1.3 to 18 percent).

The greatest sensory input to the head in terms of the number of receptor units comes from the eyes and antennae. The optic lobes are concerned with accepting input from the visual cells and, through chiasmata, ganglion cells, and elaborate synaptic systems, integrating this information. The antennal centers are much less complicated, as befits a system that does not have to deal with the same number of variables as affect the visual system. Most of the sensory input from taste is collected by the subesophageal ganglion. Most auditory, tactile, and proprioceptive input is collected by the segmental ganglia elsewhere in the body.

The corpora pedunculata and corpus centrale are clearly the great integrative centers of the brain. The former, as the elegant work of Huber and Vowles has demonstrated, contain inhibitory systems for general activity, take part in controlling walking direction, serve as the integration sites for complex instinctive behavior, and are essential for learning.

A number of people who have studied the insect nervous system, most recently Vowles (*47*), have put forward the hypothesis that the insect nervous system differs from the vertebrate at all functional levels. Because the cell bodies are small and lie at the periphery rather than surrounded by dendrites, and because the receptive areas of dendrites are smaller, it is argued that there are inherent limitations on integration. It might be concluded, according to this view, that the insects have evolved different types of nervous mechanisms. The alleged deficiencies of the neuron cannot be compensated for by increasing the number of cells. Indeed, in any case, size limits severely the availability of cell number. Not only is the number in the brain limited, the number available to the sense organs and motor systems is also limited. Vowles has suggested that as a result the perceptual world may be less rich and that the motor patterns are combinations of a few simple stereotyped movements limited by the absence of motor centers in the brain.

Systems analyses have tended in large measure to emphasize the simplicity and machine-like quality of the insect nervous system. Mittelstaedt's (*52*) meticulous analysis of prey-capture by mantids can best be expressed in his own words. "The control pattern of the entire system, at the present state of analysis, thus appears to be a chain which includes a loop within which is a second loop. If set into operation by the mechanism which provides prey recognition, the optic loop first turns the head toward the prey and the proprioceptive loop adjusts the neck muscles' activity to the load until the position 'ordered' by the optic loop is reached, so that, at final steady-state, that 'order' is accurately proportional to the deviation of the head from the body axis, and thus also to the deviation of the prey from the body axis. The 'order' is then used to determine the deviation of the strike from the body axis, which—to produce a hit—should itself be accurately proportional to the deviation of the prey from the body axis. The proportionality factor, the 'calibration' of the system, has been, on the average, correctly set during phylogeny (through survival of the best calibrated!) and apparently cannot be altered during an animal's individual life."

Other analyses of systems which serve the dynamic equilibrium of insects, as, for example, the optomotor reaction (*53*) and the haltere flight control system of flies (*54*) have also contributed greatly to our knowledge of the mechanics of control systems. All systems analyses, however, have tended to show how reflex-oriented the animal is on the one hand (for example, prey-predator relationships and optomotor reactions) and how rigidly patterned it is on the other (for example, copulation by the mantis, and singing and locomotion by the cricket). But a systems analysis commences with the premise that the object of investigation is a machine; hence the analysis is biased to demonstrate how the insect acts like a machine. In the words of Bullock (*24*): "We form the concept of a nervous system especially dominated in lower forms where learning is not so conspicuous, by ready-made combinations of springs, levers, and catches, cocked and easily triggered or self-firing to cause a complex movement, perhaps steered or shaped by sensory input."

Higher Categories of Behavior

It is perfectly true that much of the behavior of an insect is reflex and instinctive. Yet the extent to which this picture represents an accurate profile of its comprehensive behavior is weakened by the very failure to search for the higher components of behavior. The one analysis which we have attempted to make in detail—namely, the analysis of motivated behavior—has shown, even when biased against success by particularly rigorous criteria, that such behavior very probably exists. Were we to investigate "mood" we might find that insects do not differ qualitatively from vertebrates. If by "mood" we mean a situation in which responses to stimuli are different at different times as a result of retention in the central nervous system of some result of previous stimulation, or metabolic change related to feeding or egg development, then there are numerous examples of behavior which at least superficially meet the criteria and are amenable to neurological analysis. If we inquire into perception instead of arguing seriously, as some do, that insects are stimulated and do not perceive, then we can test the hypothesis that their perceptual world is impoverished compared with our own. Hassenstein's analysis of perception of movement by the weevil which shows that the animal does not react to movement of "objects" or "contours" in a shaped optical environment is a step in this direction.

The problem of pain is another Pandora's box into which one may peek cautiously. It is well known that insects respond stoically to heroic surgery. On the other hand, an entire industry has been built upon the knowledge that insects avoid repellents. Students of learning utilized the knowledge that cockroaches avoid shock. It is also known that insects submitted to trauma of various kinds (for example, insecticides, shock, hyperactivity, immobilization, excessive handling) secrete into the blood various pharmacologically active materials (*40, 55*). The fact that free nerve endings similar to the pain endings of vertebrates have not been discovered is not altogether relevant.

Pursuing the survey to its logical conclusion, we come finally to the problem of consciousness. Seeking for some physiological handhold on this problem, students of vertebrate behavior have struggled with interpreting the electroencephalogram. Electrical activity in the insect brain is, not surprisingly, generally different from that in the vertebrate brain. Whereas the latter is dominated by rhythmic slow waves and rarely shows mixed action potentials, the former exhibits spikes conspicuously and slow waves less predominately (*56*). Slow rhythmic potentials do occur, however, in those portions of the brain having structured neuropile (for example, the optic ganglia) (*49*). No attempt has been made to correlate changes in electrical activity of the brain with behavior such as sleep, anesthesia, and so on. The nearest approach is Schoonhoven's study (*57*) which reveals that the brains of certain moths are not electrically silent during diapause, that period of growth cessation during which the insect is behaviorally inactive.

All of these fragmentary bits of information are provocative in suggesting that there is more to the behavior of insects than systems analyses and unit neurological analyses reveal. We might do well to accept in principle the dualistic methodology espoused by Guttman (*8*), namely, to use, in addition to behavioristic and physiological analyses, concepts about psychological events which come to us through common sense, intuition, introspection, sensation, and perception. The idea of an extreme dichotomy that sets insects so far apart from vertebrates as to be qualitatively different is founded as much on a fear of anthropomorphism, however well disciplined, as on a paucity of data.

Perhaps these insects are little machines in a deep sleep, but looking at their rigidly armored bodies, their staring eyes, and their mute performances, one cannot help at times wondering if there is anyone inside.

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