

Insects as Experimental Material

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INSECT PHYSIOLOGY APPEARS to be passing from a phase of very rapid and often disconnected expansion into one of steady growth. Although certain isolated segments of the field were studied intensively as much as fifty years ago, the sudden expansion of the past ten to twenty years is due to an influx of many investigators from other fields. The latter have brought to the study of insect function new intellectual and physical techniques, with the result that many of the gaps have been filled and insect physiology may now be said to have some degree of organization.

Coherence in insect physiology owes much to the work of V. B. Wigglesworth who, in 1939, published the first textbook (1) on the subject. The recent or imminent appearance of two other books dealing with insect function as a whole (2, 3) will bring about further integration. Although this transition is inevitable and most valuable in any field, it should be borne in mind that insects operate on the same basic principles as the rest of living matter, and that the study of insect function is not an isolated category of knowledge with its own methods and sphere of operations. The insect physiologist recognizes that insects are in many ways peculiarly suited to the physiological approach and, in presenting his findings, recommends them as research material to other physiologists. At the same time, he shares with insect taxonomists and morphologists an interest intrinsic to insects as a group. Finally, his relations to economic entomology are comparable to those of other physiologists to medicine, the applied science often bringing to light the problems of greatest interest.

The late start of insect physiology can be traced to several causes. The phylogenetic position of insects as a specialized class, well removed from the main stem of vertebrate ancestry, may have been responsible for the feeling that analysis of insect function would add little to general physiology. Nonetheless, the basic principles of general physiology presumably apply to all forms of life, and the fact that in insects they may appear in a highly specialized form or application frequently makes them more amenable to experimental analysis. Furthermore, the small size of most insects has undoubtedly deterred many a physiologist accustomed to the frog, rat, and dog. However, modern analytic and recording techniques have largely overcome difficulties of chemical analysis and registration of responses; the problems of dissection and manipulation do not constitute major obstacles and can usually be met by mechanical devices and by prac-

tice. Actually, the small size and short life cycle characteristic of most insects turn out to be advantageous, since they greatly increase the ease of culturing and sampling of large populations, a fact long recognized by geneticists in their studies of one of the smaller flies (4).

The fact remains that the class Insecta contains a larger number of species with a wider distribution than all the rest of the Metazoa. Like their main competitor, man, many genera of insects are of recent origin, their state of evolutionary flux being indicated by the confusion of subspecies, varieties, and mutations, which plague the systematists and economic entomologists and delight the geneticists.

It was the original intent of this article to present a picture of the status of insect physiology. A first attempt in this direction produced merely a list of generalizations and a realization that the subject was already far too large and fluid to submit to a short summary of its status. Accordingly, only a few of the mechanisms by which insects maintain relations with their environment—muscles, nerves, sense organs, and behavior—are used here to illustrate present trends in insect physiology. Equally good examples can be found elsewhere in studies of the cuticle (5), the structure that most nearly characterizes arthropods, the intensive work in many laboratories on the hormonal control of molting and metamorphosis of insects, and the peculiar adaptations of insects to aquatic respiration (6). For these, and for recent work on respiration, blood, osmoregulation, digestion, and developmental physiology of insects, the general references given above and papers by Wigglesworth (7-9) should be consulted.

EXAMPLES

Insect flight. The wings of insects, unlike their analogs in other aerial animals, appear to have arisen solely in connection with flight and not from pre-existing locomotor appendages. During flight the shape of the thorax is altered by the contraction of two massive sets of muscles within, the movement being transmitted to the wings by a hinge mechanism. Flight may be studied in suspended insects, which can be made to beat their wings by removing a platform from beneath their feet. Wing-beat frequencies of several hundred per second are commonplace among flies, *Drosophila* being capable of continuous flight for 1½ hours, during which the wings may beat 1½ million times (10).

In the course of such a flight, *Drosophila* may de-

plete glycogen reserves to the extent of 3.5 per cent of its body weight (10). The extraordinary speed at which metabolic reserves are mobilized during this drastic expenditure of energy is shown by the observation that an exhausted *Drosophila* is able to resume flight 45 seconds after drinking a glucose solution, 1 μ g of glucose maintaining flight for 6.3 minutes (11). The extent of the energy expenditure during flight may be judged from the oxygen consumption, which may be as much as fifty times that of the resting insect (12, 13). Little is yet known of the mechanisms of oxygen transfer and heat dissipation or of the systems of metabolic enzymes associated with such prodigious activity, although large numbers of sarcosomes containing enzymes in concentrated form are present in the flight muscles of those insects with the highest wing-beat frequencies (14). It is also significant that the oxidation and reduction of cytochrome were first observed (15) in the flight muscles of a moth. Analyses of the aerodynamic efficiency and power output of flying insects (16) should be of immense value when they can be fully correlated with metabolic studies.

There are several reasons why insect flight should provide valuable information on the energetics of muscular performance. First, flight represents a level of activity entirely natural to the organism, and may be repeatedly started and stopped without recourse to artificial stimulation. Second, the work done in terms of air moved takes the form of a continuous output and, in spite of the magnitude of the metabolic expenditure, may be maintained at a steady level for an hour or more. Third, in the movement of the wings we see a repetition of the pattern of cyclic change or oscillation that is almost universal in living systems. Compared with activity such as the heartbeat, sexual cycle, or cortical rhythms, insect wing movements occur at a very high frequency, show all degrees of departure from a simple linear oscillation, and may be experimentally modified in both these parameters (17). It is suggested that these characteristics should make flight movements more accessible to analysis than most types of oscillation found in biological systems.

Insect flight raises many interesting questions of nerve and muscle function. The thorax of the higher insects is almost completely occupied by two sets of flight muscles, which contract at right angles to each other to alter the shape of the elastic thorax and thereby to move the wings. The frequencies at which this takes place range from 5 wing beats per second in butterflies to several hundred per second in many flies. The latter figure differs by a factor of ten from the most rapid muscle performance of vertebrates. In cockroaches, grasshoppers, dragonflies, moths, and butterflies, wing-beat frequencies are generally below 60 per second, and each contraction of the flight muscles appears to be due to a nerve impulse from the central nervous system. This, in principle, is similar to the mechanism of striated muscle excitation in other groups of animals. In flies, wasps, and beetles, in

which much higher frequencies generally (although not invariably) prevail, there may be 2-40 wing beats to each motor nerve impulse. Furthermore, impulses and wing beats are not synchronized; irregular bursts of potentials precede wing movement by as much as 50 milliseconds and cease a similar period before flight is actually terminated. The current explanation (18, 19) for this lack of synchronism is that the nerve impulses build up in the muscle pair a state of instability that eventually leads to oscillation. Oscillation is directly maintained by the tension developed in one muscle through the contraction of its antagonist; this in turn causes it to contract and develop tension in the antagonist. The oscillation of the muscle pair tends to become damped by the transfer of energy via the wings to the surrounding air, an effect which is offset during flight by the conditioning action of the irregular sequence of nerve impulses. Damping becomes apparent at the end of a flight as the whole apparatus coasts to a stop some time after the cessation of nerve impulses. Although details of its operation are still lacking, it is clear that this excitatory system obviates the need of maintaining during flight a sequence of nerve impulses at several hundred per second.

Insect ganglia and nerves. Insects have much to offer as experimental material for studies of nerve action. Metameric separation of the ganglia composing the brain and nerve cord is reflected in a considerable degree of autonomy of ganglion function. The arrangement of insect ganglia is reminiscent of the autonomic ganglia of vertebrates, although the former are concerned with locomotion and other somatic reflexes and, consequently, are more complex. The small size of insect ganglia and nerves introduces certain difficulties in connection with electrical stimulation and recording, particularly where this concerns the characteristics of conduction in axones. However, individual nerve fibers are often of considerable diameter, reaching 50 μ in certain internuncial fibers of the cockroach. From this it follows that the total number of neurons composing the nervous system is relatively small, many of the muscles being supplied by only one or two motor fibers. This makes it possible to observe central nervous activity in terms of single fiber responses without the necessity for actual isolation of the fibers involved (20). In general, insect synapses have similar properties to those of vertebrates, synapses of widely differing degrees of complexity or lability being obtainable in the same preparation (21). Cholinesterase is present in ganglia in considerable quantities (22, 23) and appears to play an essential role in synaptic conduction. Acetylcholine is also present in large quantities, although the part it plays in nerve activity is not clear. The pharmacology of the insect central nervous system presents interesting parallels and contrasts with vertebrates. Anticholinesterases have rather similar actions on synaptic conduction in both groups, whereas acetylcholine, atropine, curare, and strychnine have little or no action upon central or upon neuromuscular junctions in the cockroach (24).

Spontaneous nerve activity. This somewhat ill-defined term is used to designate activity occurring in excitable tissue after it has been completely separated from its normal nervous connections and sense organs. Twenty years ago Adrian (25) detected an irregular but sustained series of nerve impulses in the completely isolated ventral ganglia of a caterpillar. Since then spontaneous activity has been studied extensively in the isolated nervous systems of the crayfish (26) and cockroach (27), although its significance as a form of nerve activity is still uncertain. Many insect sense cells, as well as central neurons, discharge repetitively even under conditions approaching zero stimulation. This suggests that spontaneous activity constitutes not only a form of residual tonus when external stimuli are at a minimum, but also a means for greatly extending the sensitivity of excitable cells. A spontaneously active neuron may be said to lack a finite threshold, since it must sweep from a very high threshold (refractoriness) during discharge to zero threshold (excitability by thermal noise) when it reaches the point of spontaneous discharge (28). External stimulation imposed upon this rhythm could be effective from very high, down to very low, levels, triggering the discharge either earlier or later in the cycle and modulating the frequency of the rhythm. The significance of spontaneous activity in sensory and central neurons has not yet been fully appreciated, although it finds a place in the concept of endogenous activity as a factor in innate behavior (29).¹

Sensory physiology. The relative fixity of their behavioral patterns under experimental conditions and certain peculiarities of their sensory equipment make insects eminently suitable for many types of experimentation in this field. In flies and in many other insects the taste chemoreceptors are found upon the feet, as well as the mouth parts. Application to the feet of an acceptable (e.g., sweet) solution brings about extension of the proboscis into the drinking position, whereas an unacceptable solution (e.g., acid, distilled water) causes no drinking response, provided the insect has been allowed previously to drink distilled water ad libitum. The taste threshold for an acceptable substance may be measured by noting the appearance of the proboscis response when the feet of the insect are dipped successively into progressively greater concentrations of the test substance, which the insect is prevented from drinking. The rejection threshold is measured in a similar manner, the feet being dipped into a series of solutions that contain a fixed and acceptable concentration of sugar, together with various concentrations of the test substance. The unacceptability of the substance is measured in terms of the concentration which just extinguishes the proboscis response to the sugar. This technique has made it possible to measure the rejection thresholds of blowflies for extensive homologous series of various alcohols, fatty acids, aldehydes, and ketones (30), permitting for the first time an evaluation of the relation

between stimulatory effectiveness, length of carbon chain, and colligative properties of organic compounds (31). In addition to the invariant nature of the proboscis response, the fact that blowflies may be raised (2 weeks per generation) and handled by simple methods (32) in tens of thousands in the space of the average laboratory has contributed much to the scope and statistical reliability of these studies.

The location of chemoreceptors in groups upon the feet suggests experiments with this sense in insects which could not be carried out with forms in which the taste organs were either diffusely distributed or limited to the oral surfaces. In nutritional and metabolic studies an insect may be induced to drink tasteless or normally rejected solutions by dipping its feet into a sugar solution (33, 34). Adaptation, summation, and inhibition in peripheral and in central neurons may be investigated by dipping various numbers or combinations of legs into various concentrations of a test solution, or by dipping one leg into an acceptable, and another into an unacceptable, solution. Temporal factors in central nerve activity can be examined by applying to one leg a conditioning stimulus and to another a test stimulus (35).

Although the olfactory and humidity senses have not been so intensively studied, insects are promising material in this direction also. Not only do they show well-defined taxic responses to odors (36) and water vapor (37), but the sense cells concerned in these responses are located on the antennal surfaces and hence are quite accessible. The size of the antennae of many insects suggests sensory nerve fibers of considerable length, a desirable condition for examination of the afferent nerve response to chemical stimulation of the sense cells.

The reproducibility of the phototactic responses of insects in a laboratory situation has been responsible for a considerable volume of published work on intensity, flicker, form, and color discrimination (1-3, 38). The optics and anatomy of the compound eye also received much attention from early investigators. In spite of its complexity, the compound eye is much less efficient as an optical instrument than is the eye of vertebrates, although recent work has shown that it possesses two attributes that are of special interest to students of behavior and may be more widely distributed than heretofore realized. An examination of the electroretinogram of honeybees shows that these insects may be able to discriminate individual pulses produced by a flickering light, or by a pattern when moved relative to the eye, even when the pulses occur at frequencies as high as 300 per second (39). This is clearly of value to an organism moving at a high angular velocity with respect to its surroundings. Honeybees are able to utilize the polarization pattern of light refracted from the sky as a fixed point in their route-finding and orientation (38). Ants show a similar ability to discriminate the plane of polarized light (40), and the retinulae of another arthropod, the horseshoe crab, appear to be individually oriented to a particular plane of light polarization (41).

¹ See also TINBERGEN, N. *The Study of Instinct*. Oxford, Eng.: University Press (1951).

In the domain of the mechanical senses, hearing is well developed in many insects (42), although insect auditory organs probably never achieve the resolving power of the mammalian ear. The semirigid cuticle imposes special conditions on the sense organs of touch and of the position of body parts. Hinged spines serve as tactile organs, and groups of fine hairs on the cuticle are bent by the movement of one component of a joint upon the other. Torques and shearing forces developed in the cuticle by gravity or by resistance to movement are transduced into nerve impulses by groups of dome-shaped campaniform organs (43). A striking example of the function of campaniform organs is seen in the halteres of flies. Each haltere, a modified hind-wing, consists of a short shaft surmounted by a knob. During flight, muscles keep the haltere in oscillation at wing-beat frequency in a fixed plane with respect to the body axis. Any tendency of the flying insect to yaw or pitch causes in the cuticle at the haltere base a gyroscopic torque which stimulates campaniform organs in this region and initiates reflex corrective movements of the flight muscles (44). Thus the fly is provided with a gyrocompass.

Behavior. Insects have long been favorite subjects for the study of behavioral mechanisms, particularly those concerned with social activities. Their small size and relatively small radius of activity permit the unbroken observation of a complete behavioral sequence such as foraging and feeding, courtship and mating, and the like. In addition, the relative fixity of many of their taxes is undoubtedly responsible for the fact that more is known about the quantitative relation between physical and chemical gradients and orientation in insects than in other animal groups (45).

It is well known that the anthropomorphic interpretation of observations is one of the commonest sources of error in behavioral studies of animals. However, it seems to be just as erroneous to evaluate the responses, learning capacity, and memory of the subject when it has been observed only in a man-made environment, as it is to attribute to it human tendencies and desires. The casual observer becomes acquainted with the behavior of an insect such as a bee in the artificial environment of a windowpane or a restraining box, where its activities frequently consist of random seeking movements or invariant orientation with respect to some one environmental gradient such as light. Under circumstances for which its sensory and motor equipment is ill-adapted, one sense modality, usually vision, appears to dominate its activity, and the insect exhibits little capacity to modify its behavior on the basis of experience gained in moving about in this artificial environment. If the sensory equipment of an organism is considered to be adapted to its normal environment, there must be some degree of equivalence of the various sense modalities, and the fact that one sense frequently dominates the actions of insects in an experimental situation must be taken as a sign of sensory and therefore of behavioral imbalance, even though it may be a characteristic of great value in studies of sensory function. By this it

is not meant that laboratory studies of insect behavior are dispensable; merely that they will gain greatly in significance if repeatedly related to the natural environment of the subject. This viewpoint is confirmed by the following examples.

There have been a number of studies of the ability of cockroaches (46) and ants (47) to learn and to remember a maze habit. In learning this type of task insects require a great many more trials and retain a memory trace for a much shorter time than most vertebrates (47). On the other hand, solitary wasps have shown a striking capacity to learn the topography of their nesting and foraging region, being able to reorient themselves almost immediately when transported to another part of it in a dark box (48). Perhaps the most startling evidence of learning and communication by insects is to be found in the beautiful work of von Frisch (38). A worker honeybee returning to the hive from a rich source of food not only remembers and is able to retrace its path, but can communicate to other workers both the distance and the direction of the source of nectar. When surrounded by hive mates the returning bee performs a series of movements—the “waggle dance” of von Frisch—in which the speed of movement in one phase is inversely proportional to the distance of the food, and the direction taken in another phase of the dance indicates the direction of the food. The reference point both for the foraging trip and for the subsequent symbolic indication is the sun, or if this is not visible, the pattern of polarized light refracted from the sky. When the dance is performed in the darkness of the hive where neither of these reference points is available, the bee, dancing on the vertical surface of the comb, transposes the effects of light into those of gravity, moving at an angle with the vertical which is identical with the angle formed by the food source, hive, and sun. After repeating this dance the recipient bees leave the hive, and, transposing their movements once more into distance and direction, fly directly to the source of nectar.

Communities of many ant species are as complex and well organized as that of the honeybee, although the principles underlying group coherence and communication are still not too well understood. We owe to the brilliant studies of Wheeler (49) the important suggestion that group integration is based upon the exchange of regurgitated food material between the members of an ant colony. This concept of trophallaxis finds support and further development in investigations on army ants (50), whose colonies pass through regular cycles in which a nomadic phase alternates with a passive phase. The key to this group behavior is found in the condition of the developing broods, which as larvae furnish a maximal stimulative (tactual and chemical) effect on the population, maintaining a nomadic condition in the colony, and as enclosed pupae furnish only a minimal stimulative effect.

These few examples serve to illustrate the complex behavior of insects under different circumstances—an invitation to further research.

PRACTICAL CONSIDERATIONS

The work described in the preceding pages is a small segment of the field, chosen frankly because it is of particular interest to the writer. However, it serves to illustrate the general trend and vigor of insect physiology. Although this vigor is obviously dependent upon the intellectual caliber of investigators attracted to the study of insect function, there are other less obvious but equally important reasons for present activity in the field. The explosion of the atomic bomb performed a great service by largely eliminating the classical distinction between the "pure" and "applied" sciences. At about the same time industrial research introduced DDT, an insecticide unsurpassed at that time for its high toxicity to insects and low toxicity to mammals. These events appear to have convinced many concerned with the economic relations of insects to man that (1) a reasoned approach and an understanding of the operation of natural phenomena might in the long run provide more effective means for insect control than the mere empirical testing of insecticides and (2), since DDT showed a selective toxicity to arthropods, an understanding of its mode of action should make possible the development of insecticides toxic only to certain species of insects and even less toxic to man and domestic animals.

Thus insect physiology received a certain degree of moral and practical support. In the United States the Office of Scientific Research and Development was one of the first agencies to implement this attitude during the closing year of the war by contractual research, mostly relating to the mode and site of action of DDT. At the same time, several other agencies, notably the Army Chemical Corps, Quartermaster Corps, and the Public Health Service, farsightedly realized that, although their interests in insects and chemical action were of a purely practical nature, the surest way to achieve their objectives was to support studies of insect function in which the development of new insecticides was incidental. This support has continued, and at the present time the Army Chemical Corps has one of the finest laboratories in insect physiology in the United States in its Entomological Division at Edgewood, Maryland. In addition, this and other agencies support university research in insect physiology by means of contracts. Many of the state agricultural stations with their rather similar objectives are taking a comparable interest in insect function.

The intelligent attitude of these supporting agencies has eliminated much of the proverbial distrust of university workers for sponsored research, and has brought about a natural fusion of the objectives of the two groups. For instance, determination of the gustatory and olfactory thresholds of flies in relation to the structure and properties of the stimulating compounds (30, 31) has certainly enlarged our knowledge of this branch of sensory physiology, and at the same time suggests a rational basis for the synthesis of specific insect attractants and repellents (36). Work begun with the practical object of determining the

site and mode of action of agents such as DDT, diisopropyl fluorosphosphate, and hexaethyl tetraphosphate has also supplied information on sensory function (51), ganglionic activity, and the chemical factors in synaptic conduction in insects (22-24). Similarly, a knowledge of the energetics of flight (16) and of the behavioral mechanisms of insects (50) is clearly prerequisite to a rational understanding of insect migration and distribution, although these topics have an obvious intrinsic importance. Similar examples are to be found in work on the cuticle, metabolism, biochemistry, and developmental physiology of insects (1-3, 5).

At the present time great interest centers around the appearance in the field of strains of houseflies and mosquitoes highly resistant to DDT. This situation can be duplicated in the laboratory (52) when flies are subjected to the selective action of DDT for five to eight generations. The structural and functional modification conferring resistance to DDT has not yet been detected, but this practical problem offers ideal experimental material for a study of the changes that form the basis of natural selection. From the physiological viewpoint alone, the problem stretches all the way from the ultrastructure, chemistry, and physical properties of the cuticle (5) as the point of entry of DDT, to the properties of the excitable tissue affected and the nature of the enzyme systems basic to metabolism and excitability. Solution of this problem will fill many gaps in our knowledge of the physiology of insects, as well as provide a highly significant contribution to human health and welfare.

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News and Notes

European Congress of Nobel Prize Winners in Medicine

THE first European Congress of Nobel Prize Winners in Medicine was held in the town of Lindau im Bodensee June 10-14, 1951. The object of the congress was to provide a program of sufficient scientific interest and practical value to attract physicians from all parts of Germany and from neighboring countries, to meet for the purpose of stimulating a renewed interest in scientific medicine and a more congenial personal relationship. The congress was arranged by a committee of German physicians and citizens under the leadership of Karl Hein and Professor Parade, and under the protectorship of Prince Lennart Bernadotte of Sweden, whose summer home is on the Isle of Mainau im Bodensee. It is the intention of the committee to make the congress an annual event.

The scientific entertainment for the 500 physicians and their wives who attended the congress was provided by addresses presented by the Nobel prize winners, who summarized and brought up to date the work for which the prize was awarded. Addresses were given by G. Domagk, of Wuppertal, Germany; P. H. Müller, of Basel; H. Dam, of Copenhagen; A. Butenandt, of Tübingen; O. Warburg, of Germany; and W. P. Murphy, of Boston, Mass. H. von Euler, of Stockholm, a prize winner in chemistry, also attended the meetings.

In his opening address before the congress Dr. Hein stressed the acute lack of contacts among scientists in Germany and other countries since 1933 and the consequent lack of interest in, and incentive to carry on, scientific investigation, or to use the newer methods in practice. Dr. Hein felt that renewed interest and incentive should follow upon reports of their own investigative work, by men of outstanding achievement in science from various countries.

The success of the congress was evident from the

attendance and the active interest in each of the papers presented. It is the intention of the committee to invite, in rotation, as guest speakers for future congresses, the prize winners in the several fields for which Nobel established an award.

The success of future meetings should be assured by the place of meeting, the social entertainment apart from the scientific programs, and the courteous treatment accorded the guests of honor. Lindau is an interesting old city, situated on an island in the Bodensee (Lake of Constance) in Bavaria. In addition to several sight-seeing trips for the ladies, there was an evening of ballet, a dinner at Hotel Bad Schachen, which overlooks the beautiful Bodensee where the Rhine enters the lake, and an all-day steamer excursion to Meersburg Castle, the interesting island estate of Prince Lennart, and other points of interest.

WILLIAM P. MURPHY

Boston, Massachusetts

Scientists in the News

Dana K. Bailey, of the National Bureau of Standards Central Radio Propagation Laboratory, has received the Arthur S. Fleming Award as the outstanding young government man of the year. The award is given annually by the Washington (D. C.) Junior Chamber of Commerce. Mr. Bailey received the award for his contributions in the field of radio wave propagation, and for his extensive service in the field of international relations. Since 1948 he has been a U. S. technical representative at a number of meetings of agencies of the International Telecommunications Union.

The University of Maine Pulp and Paper Foundation presented George D. Bearce, of Bucksport, Maine, its 1952 Honor Award "in recognition of outstanding service to the pulp and paper industry in management