THE ORGANIZATION OF THE ARTHROPOD CENTRAL NERVOUS SYSTEM

C. A. G. WIERSMA

Biology Division, California Institute of Technology

INTRODUCTION

Central nervous systems and their functions may be studied in many ways and in a variety of different animals. Yet, the amount of research now being done on mammals, and on man in particular, far exceeds that on all other organisms. The justification for such a concentration of effort, however, may well be questioned in view of our present limited understanding, since the very complexity of these systems makes them difficult to analyze anatomically, physiologically and psychologically. For this reason a comparative approach could well be more productive. Comparative physiology has always aimed at contributing not only to a better understanding of the particular animals under study, but also to solution of the more general problems involved, which may yield more readily to investigation of particularly favorable systems.

We know that the main task of the central nervous system is to integrate the information put into it, and to produce well-coordinated efferent commands, adapted to the needs of the animal. This output from the central nervous system gives rise both to overt behavioral responses and to less obvious internal regulative changes such as circulatory adjustment, hormone production and so on. The information supplied to the central nervous system by the sensory input can, in the main, be varied only in terms of the frequency of the impulses propagated in the individual sensory fibers. Further analysis of this input must take place at higher levels.

The so-called simple reflexes are apparently the most readily understood of the central functions. Such reflexes, which may be based merely on a monosynaptic connec-

tion between primary sensory fibers and final motor fibers, are present in all animals. Because the delay times involved are the shortest possible, monosynaptic reflexes are common in quick withdrawal movements, which generally have priority over all other responses. However it is quite incorrect to picture such a reflex as an event involving only those sensory and motor fibers which take an obvious and direct part. Thus the sensory input, in addition to synapsing directly with the motor fibers, may indirectly inhibit other motor fibers, and seems invariably to stimulate interneurons which distribute information to more distant parts of the central nervous system. These facts suggest that any sensory stimulation should have effects throughout the nervous system, a situation which does not encourage hopes of a simple analysis. Whether such all-pervasive influences are important can only be investigated by the difficult task of tracking down the direct and indirect effects of a stimulus in all parts of the central nervous system.

One method of establishing such possible functional pathways is to examine the degeneration of neurons after a localized lesion. However, this approach cannot be said to establish unequivocally the physiological function of the degenerated fibers, since—for example—it cannot distinguish those that are inhibitory from those that are excitatory. Another possible approach is to use stimulating and recording techniques. This latter method will necessarily be more feasible and lead to a more complete understanding if the system to be investigated is small in terms of numbers of constituent units. The arthropod system has this advantage over the vertebrates, and still displays a comparable increase in complexity from one species to another. It seems appropriate, therefore, to sum up at this time the present state of our knowl-

edge of the functional organization of the arthropod system. Coverage here will be limited to the specific connections and functions of individual units, since several other important aspects of the subject such as synapses, neuropile, synaptic transmission, and the relations between neurological and behavioral data, are dealt with elsewhere in this volume. However it must be remembered that these factors help to give each and every interneuron in the arthropod system its specific properties.

ANATOMY AND ITS FUNCTIONAL SIGNIFICANCE

The central nervous system of arthropods consists in principle of a double chain of ganglia, connected laterally by commissures, and longitudinally by connectives. These latter consist of the axons of neurons whose cell-bodies usually lie in the periphery of each ganglion. In more highly developed species there is a tendency for the serial ganglia to form smaller or larger aggregates. Each ganglion contains two or more neuropiles which are the only known regions where synaptic (or other) transmission can take place, with the exception of the lateral synapses of the giant fibers of Crustacea and a few cases in which specific neurons are known to fuse.

The longitudinal connectives consist, as do the peripheral nerves, of bundles of axons. Similar bundles are found in the nervous systems of all higher forms, but in arthropods the number of fibers is relatively small. This parallels the relatively small number of neurons in the whole nervous system, which is estimated to be less than 100,000 when the optic ganglia are excluded. In a number of forms the connectives are long enough to make a study of their nerve impulse traffic feasible. Such analysis shows that they behave very much like peripheral nerves, and like them can be studied by splitting into smaller bundles and determining the activity of each.

This approach provides considerable insight into the types of connections which different fibers make within the central nervous system, when and how they carry their signals, and, in favorable cases, the motor effects of these signals. To date, this

particular method has, for technical reasons, only been possible in the crayfish, and it is therefore regrettable that no really good histological study of the crayfish nervous system has been made. Studies of this sort in related forms and in other arthropods have revealed a variety of interneurons with different structural connections. Several of these types can now be confidently assigned to neurons with specific functional characteristics, and it should soon be possible to know both the physiological and anatomical relations of a number of such units, thus coming closer to an understanding of their functional significance (Wiersma, 1958; Hughes and Wiersma, 1960).

Both anatomical and physiological investigations have shown that a significant proportion of the connective can be made up of primary sensory fibers, which have their cell-bodies in the periphery. A good proportion of primary sensory fibers therefore pass beyond the ganglion of the segment in which they originate. Some simply pass through it to the next ganglion without synapsing in the first, but many make connections in more than one ganglion.

The degree to which such intersegmental spreading of the sensory input takes place varies greatly, but the established extent of such spreading suggests that it might well provide a mechanism for integration at a local reflex level. For the spreading appears to be much greater between ganglia within major body regions like the abdomen than between ganglia of different tagamata like thorax and abdomen. Indeed, the larger number of nerve fibers to be observed in cross-sections of the thoracic cord (about 8,000 as against 4,000 in the commissures, and 2,400 in the abdominal cord) may be mainly due to the extensive spreading of the sensory input among the thoracic ganglia.

Some cases have been found in which the sensory input spreads to all the ganglia. The abdominal stretch receptor fibers, for example, bifurcate on entering the cord and run anteriorly as far as the circumoesophageal commissures and posteriorly into the last abdominal ganglion. The rea-

son for such great spread of sensory information is as yet unknown. The sensory input in question is known to activate the efferent inhibitory fibers going to the stretch receptor cell bodies, without needing to reach either the brain or the telson ganglion (Eckert, 1961). Since any one inhibitory fiber can react to the signals of several stretch receptor fibers, the latter must make synaptic connections in a number of ganglia. In this they are similar to the most commonly encountered type of interneuron.

Most, if not all, of the sensory fibers of the same nature, for instance hair fibers, from a single body area make synaptic connections with a common interneuron in addition to any other connections they may make. This interneuron therefore receives a great redundancy of sensory information. While this means a considerable loss in detail, it also prevents the interneuron from reacting to insignificant signals or mere noise. Thus these interneurons react only to a pattern of signals in many fibers, and not to background noise caused by accidental firing of one or more fibers.

FIRST ORDER INTERNEURONS AND THEIR CONNECTIONS

These can be conveniently divided into single- and multi-segmental interneurons, according to whether they react solely to input into one ganglion, or to that into a number of consecutive ganglia. Some (but by no means all) such interneurons in the crayfish show that this relatively simple mechanism can provide the feature of contrast, presumably in much the same way as in the *Limulus* eye (Hartline, Wagner, and Ratliff, 1956). For example, one interneuron in the abdominal cord of the crayfish has a very restricted sensory field, responding solely to a double or triple row of hairs on the dorsal side of the first segment of the telson. This interneuron will discharge continuously while the hairs in this area remain bent, but its discharge is completely suppressed by simultaneous stimulation of adjoining hairs, which thus must inhibit the generation of impulses in the interneuron in question.

A general feature of interneurons with fields restricted to one segment is that all those performing the same function for different segments tend to run together in definite bundles.

The only integrative function of most single segmental interneurons seems to be to bring together the information received from a number of similar sense organs, but a few of these neurons, perhaps only one or two for each appendage, integrate further by responding to more than one sensory modality. For example, some fibers in the crayfish respond both to hair touch and joint manipulation, and Kennedy and Preston (1960) have shown that some interneurons from the posterior part of the cord respond both to light striking the 'eye' in the last abdominal ganglion, and to touch of the telson hairs.

The multi-segmental interneurons collect information from a variable number of body segments, ranging from two to all of them. An interneuron responding to stimulation of only two segments could make all necessary connections in one ganglion, the sensory input from the two segments coming directly to the ganglion in primary sensory fibers. However this is not so for the more complex interneurons which can be experimentally shown to have synaptic connections in three or more ganglia. Impulses reaching the same interneuron in different ganglia must necessarily collide, a situation which has been demonstrated (see figure 1). Because of this interaction, the nature of the resulting discharges to both anterior and posterior centers presents itself as a real problem. Analysis of the number of impulses lost through collision has proved to be difficult, and a computer investigation along these lines is still in progress. Preliminary results indicate that preserving the functional relationship between the original inputs and final output requires that the stage, or stages, after this interneuron be pattern-sensitive in a very specific way. In the absence of such pattern sensitivity, the correct interpretation of intensity differences in the various input connections would seem to be impossible, since slight changes in the timing of input impulses re-
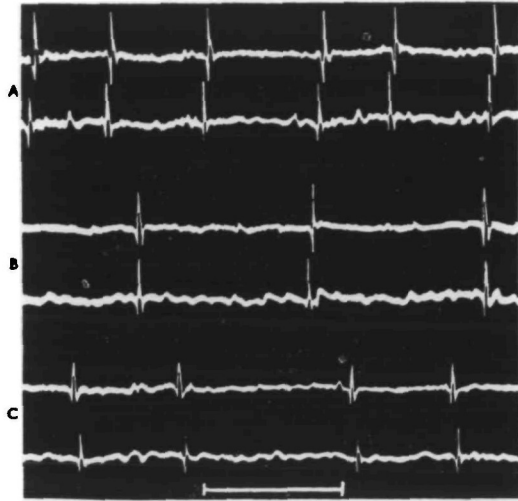
FIG. 1. Three records from two "diphasic' leads from a small bundle of fibers in a 3-4 abdominal connective of the crayfish. In each frame the upper of the two lines is from the anterior lead. Stimulation in upper frame from posterior segment, in lower frame from anterior segment, and in middle frame from simultaneous stimulation. The first and last impulses in the middle frame collide between the leads. Cuts from long records. Note the gradual reduction of action potential size between frames which developed with time. The spikes are retouched. Time 1/60 sec. (From Hughes and Wiersma, 1960a, J. Exp. Biol.)

sults in considerable increases or decreases in the total number of output impulses. An interneuron of this type cannot transmit data on stimulus location within any part of its total sensory field.

First order interneurons show strongly stereotyped reactions to stimulation of their sensory fields. Fatigue caused by the constant stimulation of one part of the sensory field does not limit the effectiveness of another sensory area in evoking impulses in the interneuron. Sometimes, however, an interneuron which responds to fields located on both sides of the body may show a different susceptibility to fatigue on the two sides. This indicates strongly that the side which fatigues more rapidly has an intervening interneuron while on the other side the input is directly from sensory fibers. Such mixtures of different-order connections can be observed in other, more complex interneurons; hence divisions into

classes on this basis must not be taken too literally.

A study of first order interneurons with bilateral inputs has shown that their connections within the central nervous system can be very different (see Fig. 2). In some cases after sectioning the interneuron, the posterior portion will respond to stimulation of the posterior sensory fields, and the anterior portion to stimulation of the anterior sensory fields. In other cases similar sectioning will result in a posterior portion which responds only to stimulation on the same side and posterior to the cut, while the anterior portion responds to all other fields, including heterolateral posterior fields. Histological features which could explain this type of difference were described long ago for crabs by Bethe (1897).

The great majority of interneurons with known input properties are first order interneurons, and, in general, little is known of the effects produced by the impulses which they propagate. A considerable number of these first order interneurons (as many as 15-20) will respond to stimulation of a single sensory field. At the same time all but two or three of these interneurons may also be activated by stimulation of a
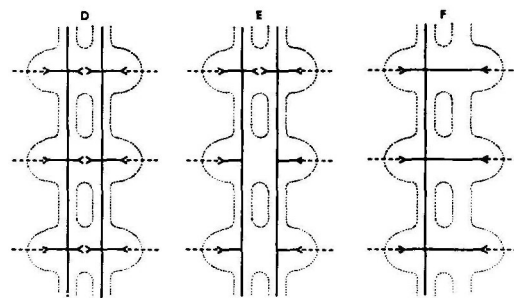

FIG. 2. Three different types of connexions (D, E, F) indicated by the findings in interneurons responding to bilateral sensory stimulation in the crayfish. In D it will be possible to record responses to stimulation of the sensory field in both portions of the interneuron after it has been sectioned. In E the posterior part of the sectioned interneuron will respond only to stimulation of the posterior region of the sensory field on that side, the anterior portion responding to the remainder of the field. In F the posterior portion will respond to the posterior part of the field, and the anterior portion to the anterior part of the field. (From Hughes and Wiersma, 1960a, J. Exp. Biol.)

number of other sensory areas. We may therefore state that although any precise information appears to be lost at higher levels of the central nervous system, a single localized stimulus will activate a complex network of pathways.

The primary information is thus subjected to a detailed analysis at the very first level of integration following the transformation of the sensory stimulus into nerve impulses. The purpose of this arrangement might be to make the sensory input available for use in a number of ways for different functions. Only in a very few instances can we readily evaluate the significance of such parallel analysis. In the optic nerves of the decapod crustacea, some of the fibers which run between the eye-stalk ganglia and the brain were found to transmit information about large objects moving in the visual field. These fibers are, no doubt, rather directly connected to the motor fibers in the legs and, in the crayfish, with the giant fibers; presumably playing a major part in causing the typical escape reactions (Waterman and Wiersma, unpublished).

On the other hand, fibers which continue to fire when certain areas are lighter than neighboring ones, must be used for other purposes, such as general visual orientation. Similar speculations can be made about hair and joint fibers, but the problem of the very great 'redundancy' of pathways will only be clarified when more is known of the central connections of the various interneurons.

RESPONSE PATTERNS OF HIGHER ORDER INTERNEURONS

Relatively little is known as yet about these fibers. Most of them appear to have rather high thresholds, or may fire only when several of the first order interneurons converging on them are simultaneously activated. In a few instances, however, they react to local sensory stimulation almost as readily as first order interneurons, even though their secondary nature is shown by the difference in their reaction after being

sectioned. In this respect the interneurons responding to bilateral fields are the most instructive. For in contrast to the first order bilateral neurons, activity in second order elements occurs in only one-half of the sectioned nerve in response to stimulation anywhere in the whole sensory field and no activity is shown in the other portion. The information must therefore be conducted to a central location, and thence be transmitted at one or more loci to the neuron under investigation. In several cases the anterior portion shows the activity, while in one case activity has been found in the posterior portion (Wiersma and Bush, in preparation).

The response of higher order interneurons depends on the activity of first order interneurons, and thus on the condition of the preparation being studied. This obviously contributes to the difficulties found in studying higher order units. In addition, inhibitory influences begin to play a very important role at this level of integration. Thus, stimulation of a distinct part of the sensory field—e.g., the homolateral legs—may readily activate the interneurons in question at certain moments, but at other times completely fail to do so. It has not yet been possible to determine either the causes of these changes in activity, or their specific interneural input.

Although functional motor relations have been determined for the secondary interneurons with high thresholds, so far no effects of activating the lower threshold fibers have been demonstrated. Possibly their influence is mainly inhibitory, and again difficult to observe. In general, it has not yet been possible to establish beyond doubt both input and output relations for any one given interneuron. The output relations must be studied by specific stimulation experiments which will be discussed in the next two sections. These sections will deal with two groups of interneurons, both of which must be stimulated at a minimum constant frequency to produce their motor effects, but which can be distinguished by the nature of these effects.

INTERNEURONS DIRECTLY RELEASING CHARACTERISTIC POSTURAL RESPONSES

The first of these groups is made up of interneurons whose stimulation results in a characteristic response which is maintained for the duration of the stimulus. In the crayfish, stimulation of certain fibers results in specific positioning of the appendages, the speed and completeness of the postural change depending on the strength of the stimulation. The best known of these fibers is the one giving rise to the 'defense reflex' of the crayfish. Here the animal raises the front of the body and the claws, and balances on the tail, maintaining this posture throughout the stimulus.

Presumably there are also inhibitory fibers with similar activity patterns, since cutting the central tracts, particularly in the brain, results in an exaggerated tonus in certain muscles of the body. Such inhibitory interneurons are probably active most of the time, being themselves inhibited on occasion. A similar picture of the central control of inhibition has been obtained in the case of the peripheral nerve fibers in the claw of the crab, *Carcinus*, (Bush, in preparation). Here repetitive stimulation of a part of the commissure causing excitation of the opener motor neuron, was found to inhibit simultaneously any reflex firing of the opener inhibitor axon, and probably also the closer motor axons. Such observations do stress the importance of central inhibitory mechanisms in overall coordination, but also show how difficult precise analysis becomes even for apparently simple reflex systems.

HIGHER ORDER INTERNEURONS GOVERNING PATTERNED MOVEMENTS

The second of these major groups consists of interneurons whose stimulation results in definite rhythmic movements, such as coordinated movements of the legs or beating of the crayfish swimmerets. Simple coordinated motor systems are present in both the cockroach (Roeder, 1948) and the dragon-fly nymph (Fielden, 1960). Stimulation of hairs on the posterior abdomen in these animals is transmitted via a limited number of interneurons to motor units which produce leg movements and an escape reaction (see figure 3). In both cases the link between the interneurons and the motor units is the most variable one in the reflex chain, and may be influenced by other factors. This system is in some ways comparable with the giant fiber system in crayfish, with the important difference that in the giant fiber system it is the link between the sensory afferents and the interneuron which is the more variable one. There is little indication that the transmission at the giant fiber-motor unit synapse can be influenced at all by other factors, though the possibility of some inhibitory mechanism cannot as yet be dismissed. Small post-synaptic potentials which arise in the giant motor fibers, either spontaneously, or as a result of stimulation of the dorsal surface of the nerve cord, have been described (Furshpan and Potter, 1958). These slow potentials depress the excitatory post-synaptic potentials arising at the giant motor synapses, but it cannot yet be stated that this is a mechanism normally involved in regulating transmission. The giant fiber system of the crayfish, however, generally does not produce movements which might be described as patterned or rhythmic, and may therefore fit better into the first group described above.

Another simple example of an interneuron commanding the release of patterned movements is known in the cicada, where a typical sound reflex is obtained by stimulating the central cut end of the caudal nerve branch (Hagiwara and Watanabe, 1956). The response consists of a pattern of alternating contractions of the main sound muscles on opposite sides, and several pattern cycles can be elicited by a single shock of sufficient strength.

The crayfish swimmeret movements provide another example which has been studied in some detail (Hughes and Wiersma, 1960). In the isolated abdomen these movements may occur spontaneously, or be elicited by suitable stimulation (e.g., pressing one of the anterior swimmerets backwards). In this system coordination depends on the sensory input produced by the move-
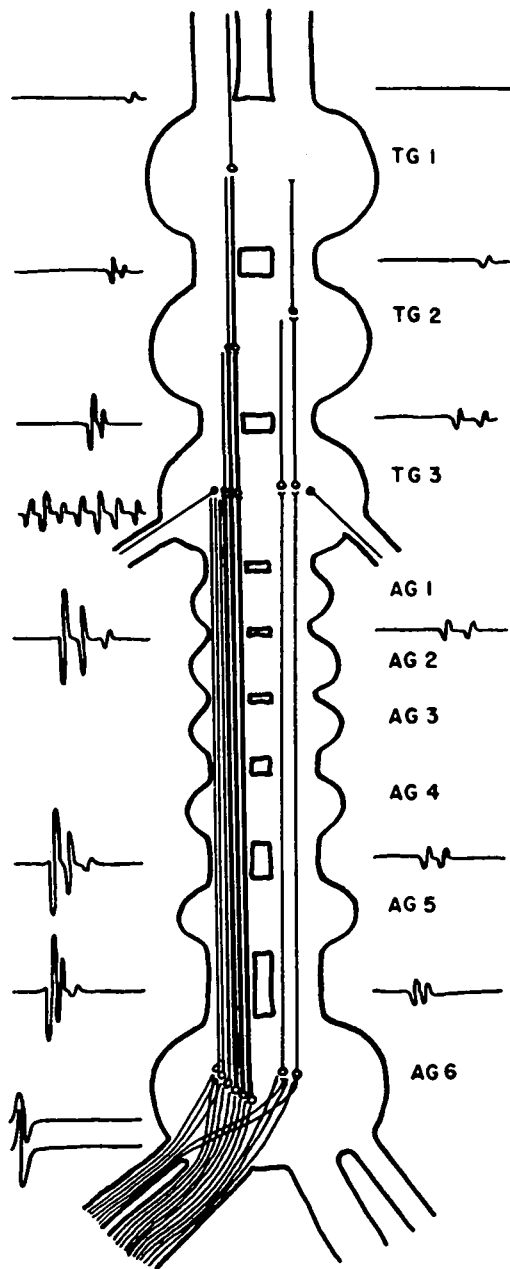
FIG. 3. Cockroach giant fibers. Schematic diagram of the ascending pathways involved in the evasion response of the cockroach. TG 1, 2, and 3; corresponding thoracic ganglia. AG 1 to 6; abdominal ganglia. The crural nerves leaving the metathoracic ganglion are included to represent efferent connections. Not shown are the reinforcing connections of the motor centers with the head ganglia. The spike response at various levels in the nervous system following an afferent stimulus is indicated diagrammatically on a base line of 10msec. (From Roeder, 1948, J. Exp. Zool.)

ments themselves. These would become uncoordinated if it were possible to sever the sensory fibers alone, as can be shown by cutting the relevant nerve roots and recording efferent activity in the cut motor fibers. The root normally supplying each swimmeret still shows rhythmic patterns of motor impulses, but these are not synchronized for the various swimmerets.

Uncoordinated movements probably originating from a similar efferent pattern can, in fact, be observed in the intact animal at times, especially when weak local stimulations are applied. It is remarkable that if one root is left intact in the above preparation, thus providing some sensory input, the motor activity in all roots will be considerably more synchronized and closer to its normal pattern. This situation closely parallels that reported for locomotor coordination in sharks and anurans (Gray, 1950).

Coordination not noticeably different from normal is obtained even when all the abdominal roots are cut, when certain interneurons in the circumoesophageal commissure are repetitively stimulated (e.g., at 60 pulses/sec). Such 'command' fibers can thus release the whole coordinated pattern without assistance from the sensory feedback. The rhythmic movements obtained will continue as long as the stimulation lasts, and in the intact animal usually for some time longer, because of the peripheral feedback mechanism. Even with the abdominal roots cut, a rhythmic discharge persists for a while after ending the stimulation of the interneuron in the circumoesophageal commissure. This may be interpreted as an after-discharge of the pacemaker center. Stimulation of other interneurons in the commissure stops the rhythmic swimmeret movements either only while the stimulus continues or for some longer period. This control of the rhythmic movements by interneurons having opposite effects is reminiscent of the nervous control of the heart.

A similar type of control has been shown for a variety of movements in insects. A detailed examination of the control of flight in locusts showed that, while peripheral feedback may influence the frequency of

wing beat, depriving the central nervous system of local sensory input from the wings does not disrupt or noticeably effect the co-ordinated movements of the wings (Wilson, 1961). This coordinated movement is apparently triggered and maintained by elements in the central nervous system which can be fired, among other ways, through stimulation of the head hairs by moving air. The same effect can be produced by stimulating the supra-oesophageal ganglion or the commissures, in preparations which exclude all sensory feedback except from the muscles in the head. Under similar conditions inhibition of the flight movements also may result from appropriate stimulation of higher centers.

This indicates that in locusts, as in the case of the crayfish swimmerets, the ultimate mechanism controlling the wings is a fixed system of neuronal pathways, which are normally coordinated so as to produce an organized rhythmic movement of the flight muscles. This mechanism is controlled by the activity of higher-order command interneurons, and can be influenced by information received through peripheral feedback.

In the nervous mechanism controlling the rhythmic respiratory movements of the cricket, each abdominal ganglion governs the expiratory and inspiratory movements of its own segment, but all the ganglia interact to produce the overall abdominal respiratory movements (Huber, 1960a). The overall regulation may in this case be controlled by interneurons which make synaptic connections in all the abdominal ganglia, probably in a way similar to those involved in crayfish swimmeret movements. The sub-oesophageal ganglion seems to function as a regulator of the frequency, since cutting its functional connections results in a permanent depression of the respiratory rhythm. Local stimulation of various parts of the protocerebrum in these animals results in respiratory movements (or inhibition of these movements) either alone or with parallel effects on locomotor movements depending on the position of the point stimulated (see Fig. 4). Hence previous claims that there are no centers for
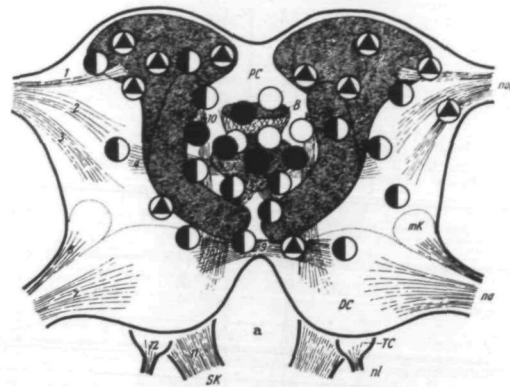

FIG. 4. Frontal view of cross-section through the brain of a cricket, showing the localized stimulation points, causing ●—respiratory enhancement: ○—respiratory inhibition; ◐—enhancement of both respiratory and locomotor movements; ▲—decrease in both respiratory and locomotor activity. PC--protocerebrum; DC—deuterocerebrum; TC--tritocerebrum; nop—optic nerve; na—antennal nerve; sk—circumoesophageal commissure; PK—mushroom body; ZK—central body. (After Huber, 1960a, Z. vergleich. Physiol.)

respiration in the insect brain are apparently incorrect, and large areas of the central nervous system must cooperate in the coordination and regulation of respiratory movements.

Rhythmic movements of the antennae and the head and palps, as well as locomotory movements, can be obtained by stimulating parts of the brain in both crickets and grasshoppers (Huber, 1959). These movements are again coordinated and have an inherent rhythmicity. The stimulation is believed to affect pre-motor interneurons which determine the duration and threshold of the different stages of the response as well as their intensity. The protocerebrum contains a control system for the head movements and the tendency to turn while walking. In addition, stimulation of certain points in the brain can result in the inhibition of motor activity. The brain also contains neurons which influence the start, duration, and strength of forward movements, and which couple this locomotion with movements of the antennae and palps. Small lesions produce no effect on the motor activity, but if both mushroom bodies are destroyed, inhibition seems to be re-
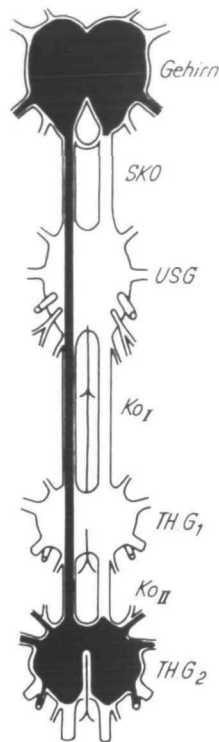
FIG. 5. Anterior part of the central nervous system of the cricket, demonstrating, in black, the regions involved in singing: the brain, one tract to the mesothoracic ganglion, and the whole of this ganglion. Sko—circumoesophageal commissures; USG—suboesophageal ganglion; Ko I, II—connectives between the lower ganglia; TH.G 1 and 2—prothoracic and mesothoracic ganglia. (From Huber, 1960b, Z. vergleich. Physiol.)

hearing organs, and the receptors of the genital apparatus, and on the basis of all this integrated sensory input, activate or inhibit sound production (see Fig. 5). These protocerebral centers are connected to the mesothoracic ganglion by way of the central body, which produces activation patterns based on the information from the two mushroom bodies (see Fig. 6). Direct stimulation of the central body gives rise to a type of squeaking unlike the usual stridulation sound. The final motor patterns resulting in the production of a particular song type and pattern, are released by the mesothoracic ganglion. If this interpretation of the control of stridulation is correct, then at least three interneurons must be intercalated between brain and motor cells.

The existence of command interneurons which have excitatory or inhibitory effects on lower centers has thus been amply demonstrated. Clearly, the integration of such command interneurons is a matter of great importance, for, as many of them produce opposing effects, there must be some mechanism to prevent their simultaneous antagonistic action. This problem will be referred to again below.

When the brain is separated from the rest of the central nervous system, the absence of inhibitory interneurons will have the most obvious effect on resulting activity. Thus a mantis with its brain removed will walk forward until exhausted, or prevented by obstacles from advancing any further,
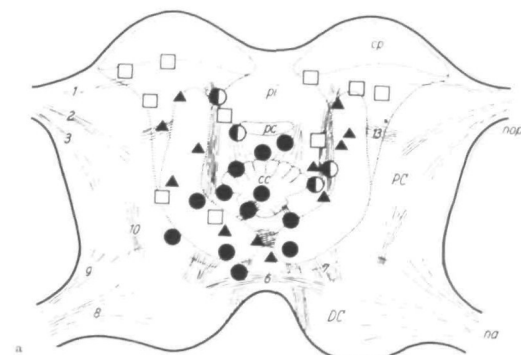
moved, since forward motion and jumping activity increase; if the central body is removed, diminished locomotion results, presumably from an absence of activation.

Stridulation in crickets is effected by the mesothoracic ganglion which controls all the twenty-eight muscles involved, and is in turn activated or inhibited by the brain (Huber, 1960b.) Stimulation of the ganglion after sectioning its connection with the brain results in rhythmic movements of the elytra, but these are somewhat abnormal and do not result in singing. Bisection of the ganglion destroys the coordination between the movements of the two elytra. Stimulation of various parts of the brain suggests that the mushroom bodies coordinate information from antennae, cerci,

FIG. 6. Frontal view of cross-section through the brain of a cricket showing the following stimulation points: ▲—normal song; ◐—rival song; ☐—inhibition of song; ●—atypical song. (After Huber, 1960b, Z. vergleich. Physiol.)

and a decapitated male mantis can make complex patterned movements resulting, under favorable circumstances, in the transfer of sperm to the female (Roeder et al., 1960). Many other similar examples could be quoted. Roeder deduced from these experiments that, in insects at least, there were widespread systems of spontaneously active efferent neurons, controlled by inhibitory systems of various types. However, in locusts the activating centers in the brain are at least as important as the inhibitory ones for the general coordination of the body (Huber, 1960), and it seems probable that this is generally the case. It appears, therefore, that any general statements about the inhibitory influence of the brain on the rest of the central nervous system must be made with caution. It is definitely not true to say that the brain normally controls the lower nervous system merely through the activation of inhibitory fibers.

CONCLUSIONS

The picture of the central nervous system gradually developing from these various observations offers a good many unexpected features. Several of these have been previously considered by workers in this field, but their existence was not clearly enough established for them to be incorporated into any more generally accepted theory. In my opinion they must now be taken into account in any attempt to explain the mechanism by which the central nervous system functions. The conception of a stepwise analyzing system with its main linkages in series, in which integration proceeds gradually from lower to higher levels, now appears both inaccurate and inadequate, although, as an idea which is relatively easy to grasp, it may remain in our thinking for some time.

Recent developments seem to point, in the arthropods at least, to a system which is to a great extent linked in parallel at all levels. Fixed, interconnected reflex pathways provide for stereotyped motor patterns which, however, may be influenced by sensory input, and are under the control of higher order fibers. The complexity of the organization of the system is indicated by the wide spread of sensory information, which is channeled simultaneously to the highest integrating levels and to efferent pathways at various levels.

It is obviously an advantage for certain response movements to be made more quickly and directly than would be possible if sensory information had to travel through an hierarchical system to the integrative centers before action could take place. This is especially true for escape and flight reactions. As one example, Maynard (1956) has shown that the spikes obtained in the various centers in the cockroach brain on stimulation of the antennae, are not causally related to the sudden jump which is the usual response to such excitation. The latency for these spikes is much greater than the latency of the giant fibers producing the movements. Hence there is a more direct connection between sensory input and effector which bypasses the higher integrative centers. In this way the muscular reaction may take place before, or at the same time as, the information reaches the brain.

However, reflexes of this type can on occasion be inhibited, or may appear without apparent sensory input, so that the higher centers can influence the activity of the reflex. It is quite feasible that all the movements made by an animal like the crayfish may be organized in a similar way, and that the function of higher centers consists essentially of activating excitatory and inhibitory command fibers controlling the reflex pathways. The available evidence shows that these command fibers are not able to vary their commands to suit the changing conditions in the periphery—they merely have the ability to fire or not to fire. Once the command has been given to the lower ganglionic centers, sensory information coming into the local reflex system will determine to what extent the command will be obeyed.

The command fibers themselves must be controlled in order to prevent conflicting instructions from being presented simultaneously. One possibility is that a higher integrating level is present, consisting of 'decision' units which determine the activity of the command fibers. The interaction

of inhibitory and excitatory command fibers might, however, provide an equally efficient control. If this is the case, the decision would be made at the level of the neurons responsible for activating a rhythmic patterned movement, or even at the level of the muscular junction. This latter certainly occurs in the control of the opener and stretcher muscles in the claw of *Carcinus* (Bush, in preparation), where signals in the inhibitor fiber are present at the same time as the motor impulses. Indeed, the activity of an inhibitory interneuron, overriding the effect of the excitatory interneuron on automatic centers in the cord, may be responsible for halting the rhythmic movements of the crayfish swimmerets.

One main question is whether the central nervous system of the arthropods can be considered to share many of its properties with the central nervous systems of other phyla, or must be regarded as highly specialized. It would be impracticable to point out all the similarities that exist, but two points are worth mentioning. Firstly, interneurons with very specific properties, a prime requirement for the mechanisms here described, have been found in molluscs (Arvanitaki and Chalazonitis, 1960), and fishes (Bennett, Crain, and Grundfest, 1959). Vertebrates have a more complex musculature and muscle innervation, necessitating the establishment of motor neuron pools, and in turn an increase in the flexibility of the control system. Even here, however, the evidence in support of automatic centers controlling rhythmic movements is very strong (e.g., von Holst, 1937). The second point is the close similarity between the responses of interneurons in the optic nerves of the frog (Lettvin, Maturana, McCulloch, and Pitts, 1959), and those in the crayfish as described above. Thus simultaneous analysis of incoming information by different interneurons, another fundamental requirement for the views expressed here, also occurs in the vertebrates.

Personally, I believe that all nervous systems will be found to function in a manner closely similar to that of arthropods. The latter can manage with a relatively few command interneurons, partly because they

have developed a rigid system of movement, which involves only a few motor fibers, and partly because the number of input channels is more limited. Many of the interneurons in the arthropods have a widespread input and output, and run for considerable distances through the system, a feature which may help to account for the fact that the arthropod system is smaller in terms of numbers of units than other systems with comparable capabilities. An intriguing possibility for future development would be to study such phenomena as learning in the arthropods, where a more basic approach might be possible.

This review is simply an initial attempt at a realistic analysis of the arthropod nervous system on the basis of present knowledge. Several additional factors are known to exist which have not been incorporated in the present discussion. Thus no attempt has been made to distinguish between interneurons with identical sensory fields, although preliminary evidence from work on the crayfish suggests that they do occur, and that they show quite different reaction types. For example, one may fire only at the start of the stimulation with a rapid initial rate and quick adaptation, while another may fire at a lower rate throughout stimulation. Such central differences resemble strongly those between peripheral fast and slow motor fibers and also similar differences in sensory fibers. The hypothesis that parallel systems, producing the same reaction but with differing velocities, are present throughout the central nervous system, might bear testing.

Another important factor in the present context is the presence of 'spontaneously' firing interneurons. It is difficult to determine exactly which these are, but any ganglion isolated together with its outgoing roots still shows impulse activity, (e.g., Roeder, 1955). Little enough is known about the genesis of these impulses and even less about their functional significance; probably this lack of knowledge constitutes the most serious deficiency in our knowledge of impulse transmission in the central nervous system. In addition, a number of factors apart from growth and differentiation may

influence the function of the central nervous system in time. Thus hormones may cause changes within the system so that the same stimulus may cause differing effects—for example, acceptance or rejection of male advances by the female. Whether these changes are caused by alterations in the rates of spontaneous impulse generation, or by changing thresholds of neurons, or possibly other factors, is an important question which still awaits an answer.

Other pertinent questions have been raised in several of the papers in this volume. Although one may wonder whether a complete insight into the workings of the central nervous system, such that all the reactions of an animal become predictable, can ever be obtained, there is no doubt that in the last years we have reached a point where the realization of such a goal is no longer beyond the bounds of reason. Interesting analogies have now been found between the functioning of the nervous system at the neuronal and at the behavioral levels. Continuation of research along all the lines developing at present must surely lead eventually to a more sophisticated approach to the whole problem of the central nervous system than has hitherto been possible.

REFERENCES

Arvanitaki, A., and N. Chalazonitis. 1958. Configurations modales de l'activité, propres à différents neurones d'un même centre. J. de Physiol. 50:122-125.

Bethe, A. 1897. Das Nervensystem von *Carcinus moenas* (3 parts). Arch. mikrosk. Anat. 50: I. 460-546; II. 589-639; III. 51:382-452.

Bennett, M. V. L., S. M. Crain, and H. Grundfest. 1959. Electrophysiology of supramedullary neurons in *Spheroides maculatus* (3 parts). J. Gen. Physiol. 43: I. 159-188; II. 189-219; III. 221-250.

Bush, B. M. H. (in preparation). Peripheral reflex inhibition in the claw of the crab, *Carcinus maenas*, L. J. Exp. Biol.

Eckert, R. O. 1961. Reflex relationships of the abdominal stretch receptors of the crayfish. I. Feedback inhibition of the receptors. J. Cell. Comp. Physiol. 57:149-162.

Fielden, A. 1960. Transmission through the last abdominal ganglion of the dragonfly nymph, *Anax imperator*. J. Exp. Biol. 37:832-844.

Furshpan, E. J., and D. D. Potter. 1958. Slow post-synaptic potentials recorded from the giant motor fiber of the crayfish. J. Physiol. 145:326-335.

Gray, J. 1950. The role of peripheral sense organs during locomotion in the vertebrates. Symp. Soc. Exp. Biol. 4:112-116.

Hagiwara, S., and A. Watanabe. 1956. Discharges in motoneurons of cicada. J. Cell. Comp. Physiol. 47:415-428.

Hartline, H. K., H. G. Wagner, and F. Ratliff. 1956. Inhibition in the eye of *Limulus*. J. Gen. Physiol. 39:651-673.

von Holst, E. 1937. Vom Wesen der Ordnung im Zentralnervensystem. Naturwissenschaften, 25: 625-631, 641-647.

Huber, F. 1959. Auslösung von Bewegungsmustern durch elektrische Reizung des Oberschlundganglions bei Orthopteren (Saltatoria: Gryllidae, Acridiidae). Verhdlg. Deutsch. Zool. Ges. 248-269.

————. 1960a. Experimentelle Untersuchungen zur nervösen Atmungsregulation der Orthopteren (Saltatoria: Gryllidae). Z. vergleich. Physiol. 43: 359-391.

————. 1960b. Untersuchungen über die Funktion des Zentralnervensystems und insbesondere des Gehirnes bei der Fortbewegung und der Lauterzeugung der Grillen. Z. vergleich. Physiol. 44:60-132.

Hughes, G. M., and C. A. G. Wiersma. 1960a. Neuronal pathways and synaptic connexions in the abdominal cord of the crayfish. J. Exp. Biol. 37: 291-307.

————. 1960b. The coordination of swimmeret movements in the crayfish, *Procambarus clarkii* (Girard). J. Exp. Biol. 37:657-670.

Kennedy, D., and J. B. Preston. 1960. Activity patterns of interneurons in the caudal ganglion of the crayfish. J. Gen. Physiol. 43:655-670.

Lettvin, J. Y., H. R. Maturana, W. S. McCulloch, and W. H. Pitts. 1959. What the frog's eye tells the frog's brain. Proc. of the IRE. 47:1940-1951.

Maynard, D. M. 1956. Electrical activity in the cockroach cerebrum. Nature 177:529-530.

Roeder, K. D. 1948. Organization of the ascending giant fiber system in the cockroach *(Periplaneta americana)*. J. Exp. Zool. 108:243-262.

————. 1955. Spontaneous activity and behavior. The Scientific Monthly 80:362-370.

Roeder, K. D., L. Tozian, and E. A. Weiant. 1960. Endogenous nerve activity and behavior in the mantis and cockroach. J. Insect Physiol. 4:45-62.

Tauc, L. 1960. Diversité des modes d'activité des cellules nerveuses du ganglion déconnecté de l'Aplysie. Compt. Rend. Soc. Biol. Paris, 154:17-21.

Wiersma, C. A. G., and B. M. H. Bush. (in preparation). On the functional connexions of neuronal units between the thoracic and abdominal cords of the crayfish, *Procambarus clarkii* (Girard).

Wilson, D. M. 1961. The central nervous control of flight in a locust. J. Exp. Biol. 38:471-490.