The Behavior of Neurons

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Research on the nervous systems of invertebrates is an important link between neurophysiology and behavior

A prerequisite for the development of scientific principles that can lead to an understanding of natural phenomena is the establishment of valid hierarchical levels. In neurobiology, neuronal behavior is one such level. To an as yet unknown extent, knowing how the nerve cells "behave" can bridge the gap between a purely neurophysiological understanding of nerve-cell function and the behavior of the whole animal.

In our laboratory we have used the stimuli and responses of single nerve cells to study the functional relationships of the nervous systems of crustaceans (crabs, crayfish, and lobsters). Among our reasons for using these animals is the fact that their behavioral repertoire is less complex than that of most insects and vertebrates. Compared to clams and snails, on the other hand, their central nervous systems are more in total command, because they have no peripheral neuronal mechanism governing local reactions—except, as in vertebrates, in the circulatory and digestive systems.

Research into the nervous systems of invertebrates like these can materially contribute to our understanding of how central nervous systems in general work, and offers good material to serve as models for studying the complex properties of "higher" functions, like the thought processes in man. It, therefore, provides an important link between neurophysiology and behavior, a subject that should be intensively pursued.

Among the crustaceans, the central nervous system of the crayfish has been best investigated. It has a relatively small number of interneurons (those fibers that connect only with other nerve fibers), and a large percentage of them have been identified and can be recognized in each individual. In addition, these interneurons are large in size, which makes it possible to detect their signals readily and even to isolate them completely. For many interneurons, it has been possible to study the effects of stimulating them individually.

The sensory interneurons are interesting because their responses indicate which features in the environment the animal selects as important. Motor reflex neurons often illustrate by their patterned output the existence of preprogrammed systems of muscle contractions. And interneurons that are high-level links in complex behavioral reactions are good monitors of the mechanism by which such reactions are obtained. Studying them may be expected to provide important insights for correlating neural and behavioral events. At present it looks as if these concepts are equally applicable to more complex nervous systems—even those of men.

It is clear that the central nervous system in crustaceans deals with incoming information from the sense organs by families of similar interneurons, whose members differ only in their sensory fields. There are a number of such families, each responding to a different type of environmental change. But within these families there are groups of interneurons that react specifically to only one aspect of a particular environmental influence. Optic interneurons, for example, react either to light level or to object motion. The fibers of each family usually have large sensory fields that overlap. This is demonstrated by the fact that one of the family usually covers all of the family's sensory field—for example, for optic interneurons, the whole eye surface—while others respond to only halves, quarters, or other fractions of it. The result is that information generated at any given point is transmitted by a number of interneurons. In other words, parallel computation is widespread in these systems.

Another important finding from our investigations concerns the change in the amount of response shown by many interneurons during different types of activity of the animal—its "moods." Many react more strongly when the animal is active than when it is at rest. For instance, when the so-called sustaining fibers of the crayfish optic nerve are stimulated by light of constant intensity, direction, and duration during rest, they will "fire," sending their messages to the brain in a predictable pattern that varies only somewhat with the amount of light adaptation. But when the animal is in a state of great excitement, as shown, for instance, by its "fight-defense" position,

sustaining fibers will fire up to five times more frequently for the same stimulus. If one were not aware of the influence of mood, one would falsely conclude that the light intensity had gone up by a very large factor.

Mood changes also have a considerable effect on the way the output system of the crayfish sends messages to its muscles. Many of the motor neurons to the various muscles, for example, increase their output when the mood of the crayfish changes, and this makes the animal more alert and ready to respond. However, some specific motor fibers are inhibited by the same mood change. For instance, switching to the defensive mood causes the muscles moving the eyecups to contract more strongly— except for the muscles that withdraw the eye, which are inhibited. This makes good sense behaviorally, because when exciting things are happening, one has to see what is going on all around.

Another fiber type of considerable behavioral interest is the space-constant group in the visual system. These fibers always look upward, even when the animal lies on its back, and therefore they represent a kind of gyroscopic system. It is likely that this group of fibers plays a major role in the orientation of the animal with regard to space.

In recent investigations we have focused more on specific "neuronal behaviors" and have tried to link these with the behavior of the animal itself. For example, at least two of the space-constant fibers have an additional function that is directly involved with specific behavioral acts. In the normal body position, the crayfish, when rapidly approached by a large object from above, will often initiate an escape response by flapping its tail. The approach of an object from underneath does not cause this response. But when the animal is lying on its side, an approach within the field of vision of either the ventral or dorsal half of the upward-looking eye will cause a flip of the tail, whereas no response can be obtained from the downward-looking eye. Quite similar observations regarding space constancy can be made for eliciting the defense reflex.

Another promising example that links neuronal activity and animal response is furnished by the family of "seeing" fibers which we have found in the rock (or spiny) lobster. In addition to the more primitive families of visual fibers like those of the crayfish, in the lobster we discovered
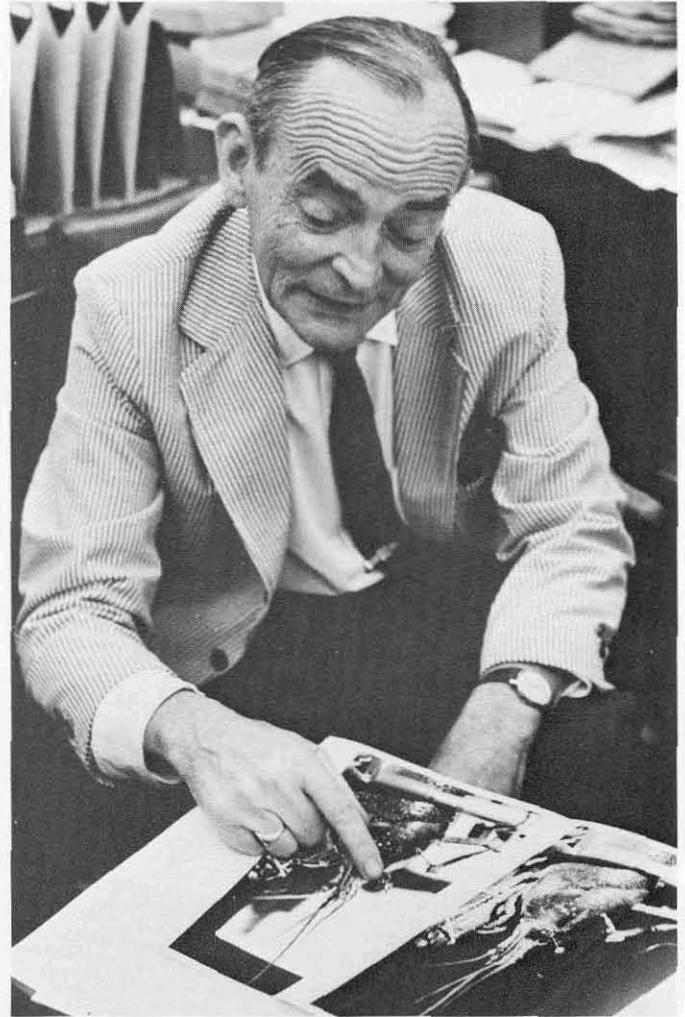
C. A. G. Wiersma, professor of biology, has been studying the nervous systems of crustaceans for many years. His most recent research on the functioning of the optic nerve in crayfish may yield important information about the physiology of vision.
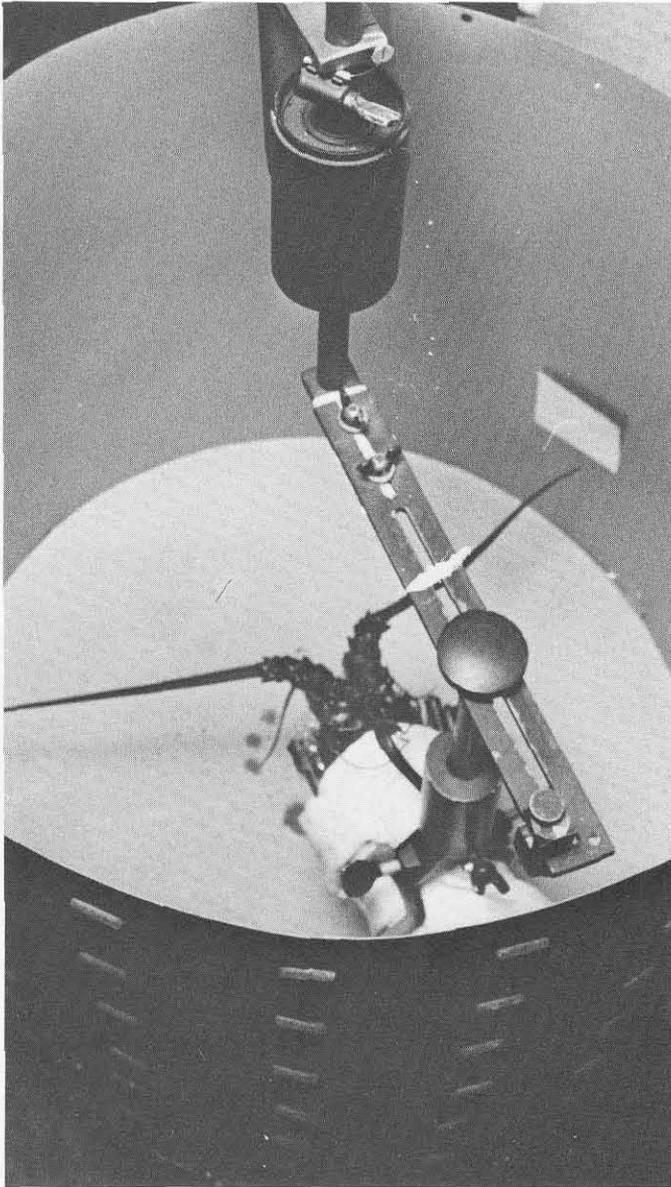
Illustrating the link between neuronal activity and animal response, a rock lobster reacts to a white square coming into the visual field by pointing an antenna at it. This crustacean is a relative of the crayfish but has additional, more sophisticated elements in its visual fibers, including seeing fibers, which are very active during this reflex.

truly higher-order elements, whose responses depend on many factors. Usually they react very well when a small target, either black or white, is brought into their excitatory field of vision at a rather slow speed. But they make little or no response to very fast or very slow movement.

The response of these seeing fibers to stationary objects is also interesting. Such non-moving objects are "seen" only by the middle part of the seeing fiber's complexly structured visual field. When an object is placed in front of this part during darkness, lighting it will cause a response, provided the dark period was short. The fiber "remembers" the old situation and compares it with the new; it fires when the object has been added, but not when it has been removed. In order to fire, however, the fiber must "pay attention" and not be distracted (inhibited) by other visual or motor response events.

As an example, in a "forward-looking" seeing fiber, the response, even to a moving target, can be suppressed by presenting another moving object around the edges of the visual field, or by stroking the abdomen or legs. Touching of the head appendages, on the other hand, arouses this fiber's interest even more and enhances its response. Since so many factors are involved in setting the re-activity, or response, level of these fibers, they are rather difficult to study in detail. Using electrodes implanted in the eye stalks, we have made recordings of the neuronal activity when the animal walks around a tank with transparent walls, and we have found that the fibers act the same under these nearly natural conditions as they do when the animal is severely restrained. There are good reasons to believe that this type of fiber (forward-looking seeing) plays an important role in initiating the reflex that causes the rock lobster to point with the tip of its antenna toward an object.

For this pointing reflex we believe that we have obtained one further link in the input-output relationship, in the form of a large interneuron. This fiber passes along incoming information of visual as well as proprioceptive origin and is thus multimodal. The movement of a small object over the eye in one direction causes the fiber to discharge, as does the movement of the antenna in the same direction. It seems likely that this is a command fiber involved in the pointing reaction. Obviously, however, additional pathways must be present to account for the accuracy of the pointing and tracking reactions.

Our previous experiments with the responses of single motor neurons that excite the eye muscles have recently led us to investigate their memory mechanism. We used a formalized version of the marine habitat of the crab in the shape of an upright metal cylinder about 18 inches in diameter and about 20 inches high. The inside of the cylinder's walls is lined with alternating black and white vertical stripes two inches wide. The cylinder can be turned clockwise and counterclockwise.

To monitor the memory responses, two minute metal electrodes are inserted through one of the eye stalks so they contact two specific nerve fibers linked with the memory. One fiber connects the memory mechanism with the muscle that moves the eye to the right; the other links with the muscle that moves the eye to the left. When nerve impulses caused by the memory mechanism stimulate one muscle, the other muscle receives no impulses and thus is deactivated. In this situation, the unstimulated muscle relaxes while the stimulated one contracts and moves the eye. The frequency of the impulses determines the strength of the signal and the amount of eye movement. The frequency ranges from zero to 50 impulses per second. The difference between the frequency of the impulses in the two nerves was used to measure the memory.

In a typical test, the animal is placed in a fixed position inside the cylinder and near its base. It is permitted to view the striped background under artificial light; then the light is turned off. In the darkness the cylinder is turned a short distance. The light is turned on again. The crab can almost invariably tell that the cylinder has been moved, and how much. To do this it must have remembered its prior position. When the background change is made during a five-second dark period, strong responses are obtained. With longer dark periods, the responses become gradually weaker for equal amounts of background displacement, but they are still quite pronounced after eight minutes.

The animals can discern very small angular movements, and with larger background changes, the response strengthens. We conclude that a number of "receiving stations," well distributed over the eye, must be activated to be "interpreted" as motion during darkness. Rotation of the animal gives the same result as background turning, and the former would be the natural stimulus.

Another question we have looked into is how long the animal must see a given background before it is remembered. In one series of experiments, the striped background at which the animals looked was turned a few degrees in darkness, exposed again for various lengths of time, and then turned back to the original position. The strength of the responses increased as the time increased. In the crab, even a half second is enough to make a difference, but the response grows in strength at least up to 20 seconds—and we always had let the animal look at the control background position for a minute or more to be sure that memory strength was near maximal.

A variation of these experiments showed the kind of struggle that goes on between "old" and "new" memories. Here the background was turned by a given number of degrees, and then—after various exposure times—returned halfway to the original position. With short exposures the old memory is strongest, with longer ones the new memory replaces the old. But at one intermediate time interval, no change in discharge occurs, indicating that the two memories are of equal strength.

We plan to continue this research, hoping to find out such things as how many memory locations are involved and where they are. At present we think there are at least four. The ease with which the system can be handled and the absence of any true learning factor (does a photographic plate learn?) make this system a valuable model for memory study.

In research on the central nervous system there has been a strong tendency to ignore the behavior of the neuron and to emphasize other aspects, but I am convinced that this approach will not be successful in explaining behavior. Investigations of neuronal behavior are likely to provide answers more quickly. One shortcoming in this area that should be rather easy to remedy is the lack of knowledge of the sum total of behavioral acts that a given species can perform. Such information is essential in order for us to be able to correlate the behavior of the neuron with that of the animal. This is true not only for invertebrates, but also for most vertebrates.

The study of the invertebrate nervous systems through the understanding of the neuron is both interesting and intellectually challenging. The field should show impressive growth in the near future and remain a subject for intensive investigation for a long time. □