Coding and Decoding in the Nervous System

Discovery of a "sixth sense" in the humble crayfish opens up new avenues in neurophysiological research

by C. A. G. Wiersma

One of the many ways in which man is distinguished from other organisms is in the extraordinary development of his nervous system. How is the nervous system constructed? How does it function? These are questions of tremendous importance for an understanding of the relation of mind and body. Answers are being sought at levels of research ranging all the way from individual molecules to the whole organism.

For over 25 years, the Institute's department of neurophysiology has been studying how messages are transmitted through the nerves, from the sense organs to the brain, and back to the muscles. In the vertebrates, and more especially in mammals, the number of nerve fibers present is staggeringly large, making it difficult to trace the fate of a signal in any one channel. However, the crayfish, whose nerve cells are relatively large in size and relatively small in number, was found to be an ideal subject for such basic studies.

In recent months, a new type of sensation has been discovered in the crayfish which is tentatively labeled a "sixth sense." This sense is unique because information is transmitted in a different way than in other sense organs. The nerve cell fibers involved, which are called the unidirectional movement fibers, collaborate in the control of the leg joints of the crayfish.

A nerve is a bundle of separate nerve fibers, each capable of transmitting a signal either to or from the nervous system (the brain and spinal cord). All sensations, all voluntary muscle contractions, and many other activities depend on this conduction of nerve impulses. There are strong reasons to believe that in any one nerve fiber each nerve impulse is like any other, so the only variable for transmitting different messages is the time sequence in which the impulses follow each other.

Like other arthropods, the crayfish carries out the "business of living" with a relatively small number of nerve cells (below 100,000). Even so, this animal seems to react and adjust to the environment as adequately as the frog, whose nerve cells may be numbered in the millions. In both arthropods and vertebrates, the more highly developed forms (insects and mammals) show considerable refinement in their reactions without proportional increases in the total number of nerve cells. The advantage of studying the less-complexly-reacting crayfish lies, as in the case of the frog, in the greater predictability of the reflex responses. In the study of the crayfish, one may, of course, encounter processes which are absent as such in the vertebrates. An understanding of these processes may lead to the finding of related ones in vertebrate nervous systems.

Unique decoding

The first discovery to call attention to the crayfish as a useful experimental animal was the peculiarity in transmission between its motor nerve impulses and the contraction of its muscle fibers. An outstanding feature of the arthropod nervous system is the small number of motor fibers innervating its muscles. Even such a large muscle as the one that closes the claw of the lobster, which consists of many thousands of muscle fibers, receives only two motor fibers. A comparably large vertebrate muscle, on the other hand, is innervated by hundreds of nerve fibers. In these muscles, speed and strength of contraction are to a large extent regulated by a variation in the number of motor fibers activitated at a given moment. Obviously, such a mechanism is quite ineffective when there are only two motor fibers; in fact, since each motor fiber in many crustacean muscles innervates *all* of the muscle fibers, it would not operate at all. But it turns out that when the same sequence of motor impulses is induced by electrical stimulation of the two fibers in turn, the resulting contractions are quite different. This means that at the neuromuscular junction the similar signals are decoded in quite different ways. It has been possible to show that each individual muscle fiber possesses this decoding property; but how this comes about is not completely understood yet.

The most likely hypothesis at present is that a chemical transmitter substance is released at the junctions, and that there is a slight, but significant, difference in the composition of the chemicals released by the two motor nerve fibers. It will, of course, be necessary to study such transmitters in isolation before further light can be thrown on these intriguing differences. The importance of such investigations is the insight they offer into the elusive coupling process between the activation and the contraction of muscle fibers.

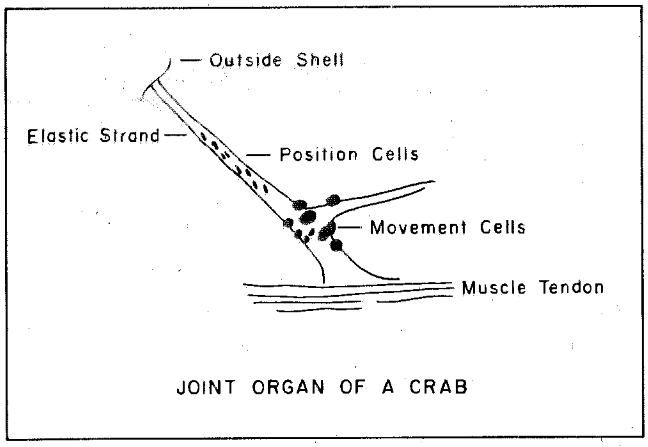
In addition to motor nerve fibers, crayfish muscles receive nerve fibers from the central nervous system which *inhibit* contraction. So far, decapod crustaceans such as crayfishes, lobsters and crabs are the only animals in which this inhibitory mechanism has been found to be present. With these animals it is possible to isolate and stimulate single inhibitory fibers along with the motor fibers for given muscles. Such nerve-muscle preparations allow precise study of the mechanism of inhibition far more easily than similar complex inhibitory mechanisms in the vertebrate central nervous system.

Chemical transmitters

According to present views, inhibition also comes about by the release at the nerve endings of a chemical transmitter whose action interferes in a complex manner with that of the excitatory transmitter substance. Thus, by liberating two different types of substances, the decoding of identical impulse series in the two kinds of fibers leads to opposite effects in the muscle fiber.

The investigation of peripheral neural mechanisms in the crayfish has also contributed significantly to the problem of coding environmental changes into nerve impulse sequences. In the abdomen of the crayfish there are seven flexible joints, each provided with two pairs of sense organs called the muscular stretch receptor organs. Each indicates, by the firing of a single sensory fiber, how far a small specialized muscle is stretched, and, in general, the relative position of two segments of shell. Though the two organs on one side are similarly built, they differ quite noticeably in their reactions to flexion. If a shell segment is bent quickly to a certain degree with respect to the one in front, one sense organ (the slow receptor) will keep firing at an almost undiminished rate for more than an hour, or as long as the position is maintained. The other organ (the fast receptor) will adapt and become quiet after a burst of impulses, lasting not more than a minute. The stretch receptors, when properly isolated, consist of a smaller amount of living substance than any other isolated piece of tissue with the capacity of generating action potentials. For this reason they are particularly useful for investigating such problems as the action of drugs on generation of impulses.

Crayfish stretch receptors have still another useful feature. They are the only receptors so far known which receive an inhibitory innervation. By stimulation of an inhibitory fiber, it is possible to diminish the sensitivity of these receptors at will, and thus to adjust their sensitivity. Similar suppression of incoming sensory impulses must also occur regularly in the human central nervous system, such as when we exclude certain noises from our consciousness. However,



Like the crayfish, the crab is another of the decapod crustaceans which has a relatively small number of nerve cells, some large in size. This simple type of system is useful in studying how messages are transmitted through the nerves.

these complex phenomena are completely central in the vertebrate nervous system, and thus harder to study. It is interesting to note that as yet it is not known what use the crayfish makes of its peripheral inhibitory mechanism.

The "sixth sense"

The coding of stimuli into nerve impulses in these crayfish stretch receptors is similar to most known sensory fibers. That is, the frequency is proportional to the logarithm of the stimulus strength. The new organ or "sixth sense" which has been found in the crayfish and other decapod crustacea can be considered as a new type of sensation because of the remarkable method by which the stimulus is transformed into an impulse sequence.

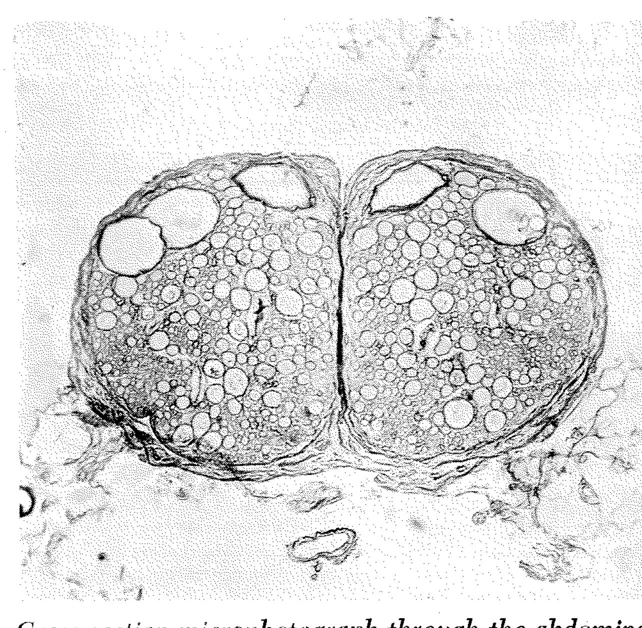
The drawing above illustrates how the nerve cell bodies of this organ are attached to an elastic strand which spans the joints. Each of the sense organs is able to fire at least four quite different types of discharges into corresponding nerve fibers. By isolation of the fibers it was found that these are: a) sensory fibers which signal position to one side of the midpoint of the arc through which the joint can move; b) fibers which signal the position only to the other side; c) fibers which discharge during movement anywhere over the whole arc in one direction; d) fibers which signal movement in the opposite direction.

The position fibers respond with outputs similar to those described for the stretch receptors – that is, their frequency gradually increases as more extreme positions are reached. Instead of two there are many of these fibers for each organ, and all of these appear to be appreciably different with regard to the positions at which they start to fire. They also differ in adaption rates; some fire for very long times at constant frequencies, while others adapt very quickly.

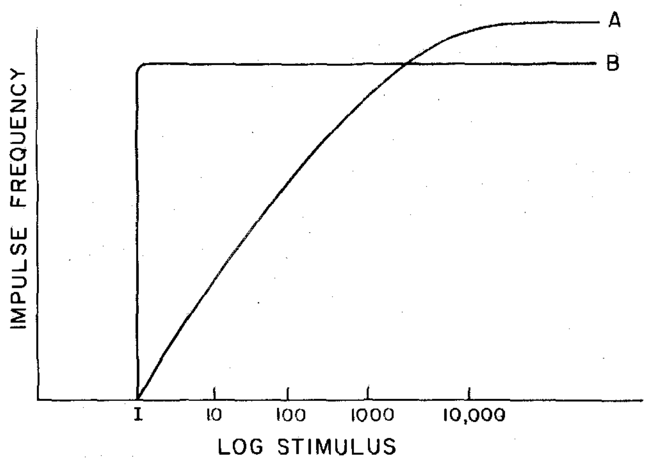
The "movement" fibers, on the other hand, have a completely different type of response which is especially evident in the most sensitive ones. They fire at constant rates once the movement is slightly faster than threshold and stop firing as soon as movement ceases. For instance, such a fiber will fire 40 impulses per second when the joint is moved at an angular speed of 1° per second, and at exactly the same rate when the motion is more than a thousand times faster. For the total possible movement of the joint from one extreme to the other (an angle of about 120°) 4800 impulses will result for the first speed, whereas only 4 impulses will be fired at the second speed. These 4 impulses cannot convey any other information than the first 4 of the 4800, and therefore the only information that can be extracted from these signals is how *long* movement takes place – not how *far* or at what *speed*. It is true that, for speeds between 0.6 and 1° per second, the fiber under discussion does not fire at its maximum speed, and that impulses are separated by longer time intervals. However, the basic frequency still remains 40 per second, and the difference is that random impulses drop out as speed decreases. As a result, the oscilloscope record obtained looks very much like a comb in which teeth are randomly missing.

Movement fibers

From one such sense organ some six fibers sensitive to movement in one direction can be obtained, each of which has a different threshold and fires at a different maximum frequency. Though their maximum frequency is higher, the most insensitive fibers produce only 12 impulses for a single maximal motion at



Cross-section microphotograph through the abdominal cord of a crayfish. Giant fibers are at the top and smaller interneurons occur in greater numbers throughout.



The unidirectional fibers of the crayfish transmit their information in a different way from fibers in other sense organs. A *shows the relation found in most sense organs;* B *the relation found in the new type of sensation.*

the optimal speed. Because of these differences in threshold between the movement fibers, the organ as a whole can provide information which denotes movements at different speeds to the central nervous system. But it should be noted that it will depend on the central connections whether this information is really used, and if so, in what way. In the diagram above, the difference between the relation of impulse frequency and stimulus strength of these fibers and the "normal" type is given.

The central nervous system

The central nervous system of the crayfish has also been found to be of considerable interest and usefulness. One of the main reasons for this is the small number of interneurons, those fibers which connect the nerve fibers with each other. In addition, these interneurons are large in size, which makes it possible to detect their signals, or even to isolate them completely. It is thus possible to study the effect of stimulating them individually.

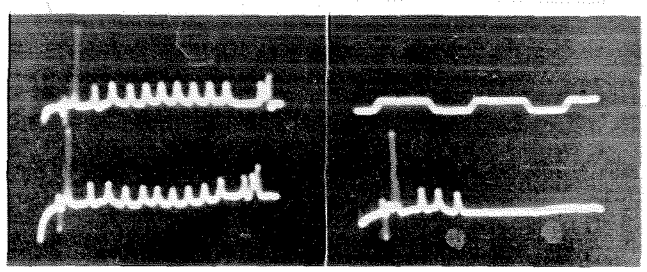
Especially easy to isolate are the four giant fibers, which serve the animal in the escape reaction of backward swimming. By stimulating these and recording from motor fibers, it has been shown that transmission and decoding of their impulses to the motor fibers at the synapses offers a number of interesting features. In general, transmission is much more effective at these synapses than is usual. For the motor nerve fibers causing the strong tail flexion, a one-to-one transmission relation is present. A remarkable feature of these synapses is that they may be wholly electrical, without a chemical transmitter substance. The membrane separating the two fibers has the property of a rectifier, permitting current flow in only one direction. This serves as an assurance against stimulation in the wrong direction.

The synapses of the giant fibers with certain motor fibers show that a single impulse in the one can lead to a repetitive discharge in the other. This multiplication of the signal can result in as many as 10 to 15 motor impulses from a single action potential in the giant fiber (below). But most crayfish interneurons, like those of other animals, transmit only after a number of impulses have reached them. In both of these latter types of transmissions, the liberation of chemical transmitter substance must be involved.

In the crayfish central nervous system a single interneuron is able to spread its impulses over wide areas because it has many endings, widely separated, where synapses exist with other fibers. Even more remarkable is the fact that there are also many interneurons which can receive impulses at very different levels. This leads to collision of impulses in the main axon of such fibers, when they are stimulated at two places at the same time. As a result, the output of such fibers – that is, the impulses reaching the place where they synapse with following fibers – becomes difficult to predict.

An unexpected finding

Interneurons can receive inputs from many sources, differing in the type of sensation or in the localization of the sensation. Remarkably enough there are many interneurons in the crayfish which do the latter, so that there appears to be a plethora of this type of combination – whereas the "integration" of different types of sensation, though present, is much more poorly represented. This unexpected finding may be important for views concerning the structure of such systems. However, before the mechanisms present can be understood, it will be necessary to do more than investigate the reactions of specific interneurons. It will be necessary to know the subsequent consequences of these impulses in the higher parts of the nervous system before their function can become evident. This is a difficult task in any animal, but if the coding and decoding processes taking place in central nervous systems can ever be completely analyzed, those of the crayfish could be the first.



A photographic record of responses in the motor nerve of a crayfish. Left, repetitive discharges in two symmetrical nerves – right, discharge in a single nerve after fatigue at the synapse. Time, 60 cycles per second.