FORTY-SIXTH
JAMES ARTHUR LECTURE ON
THE EVOLUTION OF THE HUMAN BRAIN
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WHAT SQUIDS AND OCTOPUSES TELL US ABOUT BRAINS AND MEMORIES

JOHN Z. YOUNG

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*Elliot S. Valenstein, *Persistent Problems in the Physical Control of the Brain*; May 16, 1974

[a]Marcel Kinsbourne, *Development and Evolution of the Neural Basis of Language*; April 10, 1975

*John Z. Young, *What Squids and Octopuses Tell Us About Brains and Memories*, May 13, 1976

[a]Unpublished.

*Published versions of these lectures can be obtained from The American Museum of Natural History, Central Park West at 79th St., New York, N. Y. 10024.

† Published version: *The Brain in Hominid Evolution*, New York: Columbia University Press, 1971.

WHAT SQUIDS AND OCTOPUSES TELL US ABOUT BRAINS AND MEMORIES

NEW TECHNIQUES FOR STUDIES OF THE BRAIN

To reach a better understanding of the human brain we need to develop new ways of thinking and talking about the nervous system in general. All our knowledge of nerve fibers and their synapses proves to be something of a disappointment when we try to explain complex forms of behavior, such as that of man. I have believed for many years that to overcome this difficulty we must try to describe as fully as possible the behavior patterns and the whole nervous system. When I began research, I thought that it might be possible to do this for lampreys and after making some studies went so far as to write what would now be called a research program with this in view. But on further consideration, I decided that both the behavior and structure of the brain of these animals were too difficult to study, mainly for technical reasons. Moreover in 1929, for the first time, I became acquainted with octopuses and squids and quite soon decided that their nervous systems seemed likely to provide sufficient complexity to be interesting and sufficient accessibility for anatomical study and experiment. It is not too much to make the claim that this hope was well founded, as we now have some understanding of all parts of the cephalopod nervous system. We also have a lot of information about their behavioral capacities—at least in the laboratory; less, unfortunately, in their native state in the sea.

It may seem to be a vain and unjustified claim that we understand cephalopod brains so well. Of course, there is an immense amount that we should like to know. But I hope that the effort to substantiate this claim may serve to bring out both the extent and the limitations of our knowledge of all brains, including that of man. It may show how what we mean by "understanding the brain" has changed over the last 50 years since this research began. This may prove to be quite a useful exercise not only in the history of neuroscience but in the study of the relations of science and technology in general.

We can recognize four major changes of scientific method and capabilities since 1929 that have especially influenced neurology.

1. Reliable methods of recording small changes in electrical activity have become widely available. With these we can follow events in nerves and brains with a very high degree of resolution in time. Resolution in space can also be precise, but is limited to a few places in the brain at a time.
2. Electronmicroscopy has provided us with the power to study the structure and organization of neurons with a very high degree of resolution in space. This, unfortunately, is possible only by accepting very poor resolution in time. We cannot follow changes from moment to moment with the electron microscope.
3. Chromatography provides us with the power to study the microchemical composition of tissues, estimating quantities of substances that are present in very small amounts, though again with rather poor resolution in both space and time. Fluorescence microscopy has also been particularly helpful in the study of the nervous system because of its capacity to reveal selectively the course of tracts containing biologically active amines.
4. Finally, during this period mankind has enormously enlarged his mathematical powers of computation. Computers help us to bring together the vast masses of data provided by other techniques. Besides their help with arithmetical operations, it is even more important that computers have led to great advances in our understanding of the operations of communication and control which, until recently, were considered only by using the language of subjective psychology.

Knowledge of the nervous system has profited from these advances. My own detailed contributions have mostly been in humbler fields, using older techniques of histology and psychology. But through developments that we have sponsored in the Department of Anatomy at University College, London, I have been near the beginning of several of these four major new developments of technique and have been able to find helpers in applying them to cephalopods.

THE BRAIN AS A HIERARCHICAL SOMATOTOPIC COMPUTER

Our aim is to try to understand the nervous system as a whole. Let us therefore begin with the last of the new techniques mentioned. Cybernetics can tell us how to think of the brain as a hierarchical computer, somatotopically organized (Arbib, 1972). The idea of hierarchy in the nervous system was introduced by the clinician Hughlings Jackson long ago, and cybernetic analysis shows that it is really an essential feature of any organization that uses much information to accomplish a purpose, whether it be an army or an octopus. Hierarchy allows each level to receive only that part of the information that is relevant for the decisions it must take. This is magnificently illustrated by octopuses (fig. 1). Each of the eight arms carries hundreds of highly mobile suckers and the movements of

FIG. 1. An octopus swimming forward to attack a crab.

these, and of the whole arm, are controlled by nerve cells lying in ganglia within the arm. There are altogether 350 million cells in the arms as compared with only 150 million in all the rest of the nervous system (Young, 1971). The suckers are the enlisted men of the cerebral army, and their local nerve cells are the noncommissioned officers. Individual isolated arms are capable of quite complicated coordinated movements, for example acting either to draw objects in or to reject them. These peripheral centers are thus the next layer of members of the hierarchy and can act independently. They are the regiments of the cerebral army, and the nerve cells placed along the center of each arm are the junior officers who control them. They receive information from individual suckers and order them to act in particular sequences.

The brain contains lower motor centers, comparable with our own spinal cord (fig. 2), and these control movements of all the arms when working together and of the mantle, which acts by jet propulsion. Electrical stimulation of these centers will produce movements of the relevant parts, including changes of color by the chromatophores (Boycott and Young 1950; Boycott, 1961). To pursue our analogy we here have regimental and brigade headquarters. They receive relevant information from the arms and send orders to them. However, these centers normally operate under the control of still higher motor centers in the basal supraoesophageal lobes. These basal lobes have structure strikingly like our own cerebellum, but before we can understand their working we must begin to think more carefully about what tasks the nervous system has to do, and what we mean when we say that it sends information, instructions, or commands.

COMMUNICATION AND CONTROL BY THE NERVOUS SYSTEM

Since the last century it has been usual to think of the nerves as agents of communication, following the analogy of telegraph wires. But what do they communicate? Neurophysiologists have been cautious and confused about this ever since the time Des-

FIG. 2. Longitudinal sagittal section of the brain of an octopus.

cartes spoke of nerves with the analogy of pulling on wires to ring bells or of animal spirits traveling along hollow tubes.

During the last century and the present one, physiologists have mostly described the activity of nerves by using unquestioningly the phrases "nerve impulse" or "action potential," but now we can see that these are rather ambiguous and indeed evasive terms. This will sound like rank heresy, especially coming from me since the giant nerve fibers of the squid have told us more about nerve impulses than any other nerve fibers have done (fig. 3). I came upon them by chance while studying squid ganglia for another purpose. The cells related to them had indeed been seen by Williams in 1909. But there had been no further mention of the cells in the literature, and no one had seen the giant fibers themselves. In 1936 at Woods Hole we were able to prove that these huge channels are nerve fibers and figure 4 shows some of the earliest records of their action potentials. The function of these enormous nerves is to elicit contraction of the sac that produces the propulsive jet. The arrangement ingeniously provides that both sides of the mantle and its nearer and distant parts all contract together (fig. 5).

If the function is so well understood, what do I mean by saying that the concept of an impulse or action potential is ambiguous? What's in a name? In this context of the giant fiber system I agree that it does not matter much. An activity spreads

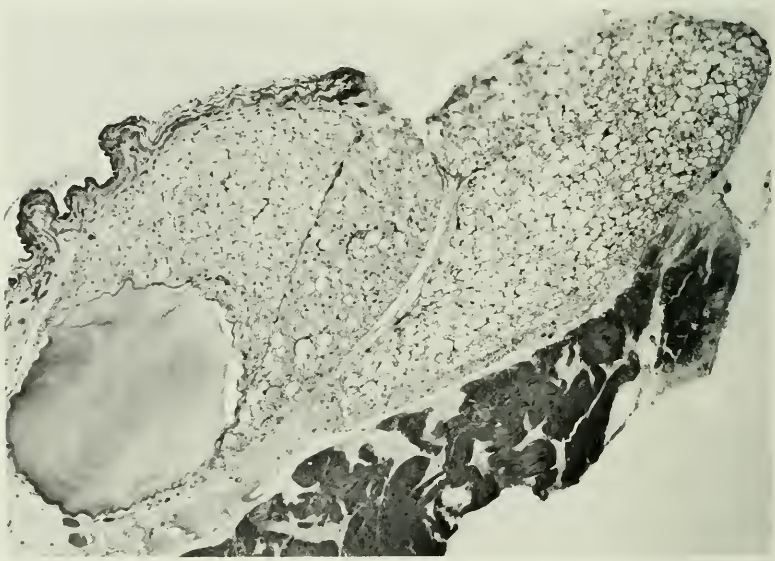

FIG. 3. Transverse section of one of the stellar nerves of a squid. There are many small nerve fibers and one giant fiber.

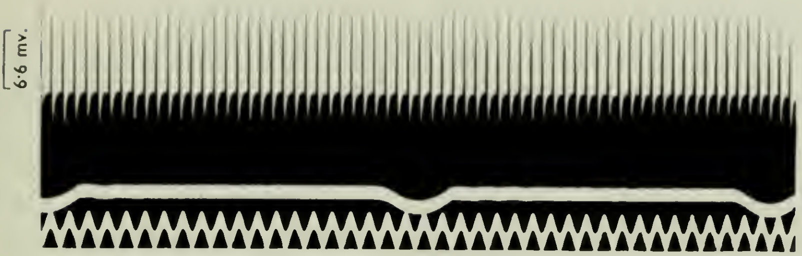

FIG. 4. Oscillograph record of the electrical changes accompanying a sequence of nerve impulses in a squid's giant nerve fiber. The discharge has been set off by placing oxalic acid on one end of the fiber. Note that the impulses are all the same height. The time-markers show 1/5 or 1/100th sec.

along the nerve fibers and we can tell rather precisely how it is initiated by a synapse in the stellate ganglion and propagated to start off a muscular contraction. We can even show that one nerve impulse produces one pulse of the jet, so we can say that the action of single cells in the nervous system produces a particular behavioral act by the whole squid. This is good progress in understanding. We can go further and apply it to mammals where, in a monkey trained to press a lever, single cells of the cerebral cortex show electrical activity before the movement begins (Evarts et al., 1971). Thus we get a good idea of how the nervous system is made up of nerve cells each of which has a distinct function.

This sounds fine and is indeed true. The principle on which all nervous systems are built is that of multichannel communication. Each nerve fiber carries only one sort of message, either inward from a sense organ or outward to produce some action by a muscle or gland. Each fiber thus carries only a small amount of information. To carry large amounts of information inward and to produce varied and subtle behavior, very large numbers of fibers are needed, each having a different "function." The trouble is that in the more interesting parts of the brain we cannot specify what the "function" is. So when we say that when we see red certain nerve fibers from the eye transmit something called nerve impulses we do not really know what we are saying. In what sense do nerve impulses transmit redness?

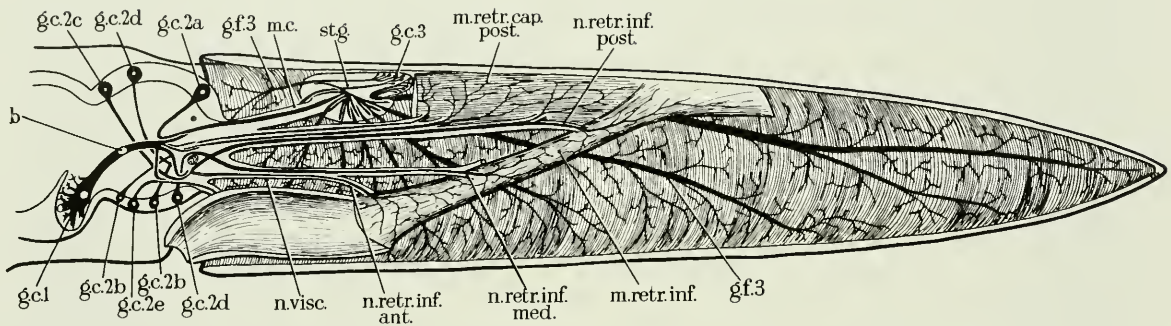

FIG. 5. Diagram of the giant nerve fiber system of the squid. Three links are involved. gc_1 is the giant cell (one on each side), which is activated by signals from the eyes, statocyst and elsewhere. Nerve impulses pass along its axon and across the bridge, b, so that the two sides always work together. The fiber then branches and makes synaptic contact with the various second-order giant fibers, labeled g.c.2a, 2b,2c, etc. These pass signals to the various muscles that are involved in the jet. The chief of these is g.c.2a, whose fiber passes in the mantle connective (m.c.) to the stellate ganglion (st.g). Here it ends but makes contact with a whole set of third-order giant fibers (g.c.3) which activate the muscles of the mantle, making the jet (from Young, 1939).

To answer this we must look more carefully at what we mean when we say that the nervous system serves for communication. We are using words borrowed from human activities in which a sender has a message calling for some action that he expects from a recipient. He passes signals in what we call a code along a channel to the receiver, who decodes it and selects the required action from the repertoire, or set, of programs available. There are very many fascinating things we could say about this situation. For the present, notice firstly that the activity of communication presupposes an aim or purpose that is to be achieved by choosing the right program from a set. Further it makes use of some arbitrary code of signals, preset by past history and "understood" by transmitter and receiver. Living things are the only systems that we know of that maintain themselves by communication in this way. So what we are doing is to use the words that have been developed to describe human social life to describe all living things. For the present we are concentrating on nervous messages themselves, and we notice that the analogy suggests that they be called signals in a code. Physiologists are beginning to talk about nerve impulses in this way but curiously enough the physiologists who win Nobel Prizes for the study of nerve fibers seldom, or never, use words such as "code" or "symbol." They stick to the dear old terms "nerve impulse" and "action potential." They have indeed been able to find out a very great deal about the physical changes that are involved in the transmission of the nerve message, without thinking much about what the message communicates. To be unkind one might say it was like giving a Nobel Prize for Literature to people who had advanced knowledge of typewriters, or of ink, or perhaps of radio transmission! I may say that many of my best friends are Nobel Prize winners—at least they have been until now!

But there are two further turns of the screw that physiologists must suffer. The significance of signals in a code is that they symbolize the matters to be communicated. If we are to describe the effects of our nerve impulses properly, in this analogy we must say that they are significant because they are symbols, that is, they stand for or represent either some event in the outside world or some inner need or some action to be performed at the decoding end of a communication channel. We say that a sign or a signal becomes a symbol or representation for something else when it has the effect upon us of that something. A traditional picture of a horse symbolizes horse for us; but the horse in Picasso's "Guernica" does more, it symbolizes also fear and horror.

I claim, therefore, that we shall learn to understand better how the nervous system works if we consider how the operations of each part of it represent or symbolize either some change in the inner or outside world or some instruction for action, passing outward from the brain to the muscles or glands. Let us then see what the various parts of the nervous system in our cephalopods serve to symbolize.

SYMBOLS FOR GRAVITY AND MOVEMENT

Cephalopods, like other animals, arrange their behavior in such a way as to respect the demands of gravity. To be able to do this they have within themselves parts which by their physical structure symbolize gravity and movement. These are, as it were, little models of those features of the universe. Cephalopod statocysts are based on principles surprisingly similar to those used by vertebrates, including man (fig. 6). Like our own inner ear, they combine receptors for maintaining orientation with respect to gravity with others that are sensitive to the angular accelerations due to movement of the animals.

The gravity receptors illustrate well the principles involved in symbolization. To meet the task of correct orientation in relation to the earth's surface, there is present in the statocyst a little model to represent gravity, a stone hanging upon sensory hairs. These hairs send streams of action potentials whose pattern thus symbolizes the position of the animal in relation to gravity. The connections of these nerve fibers must be meticulously arranged to ensure that the various muscles pull to pre-

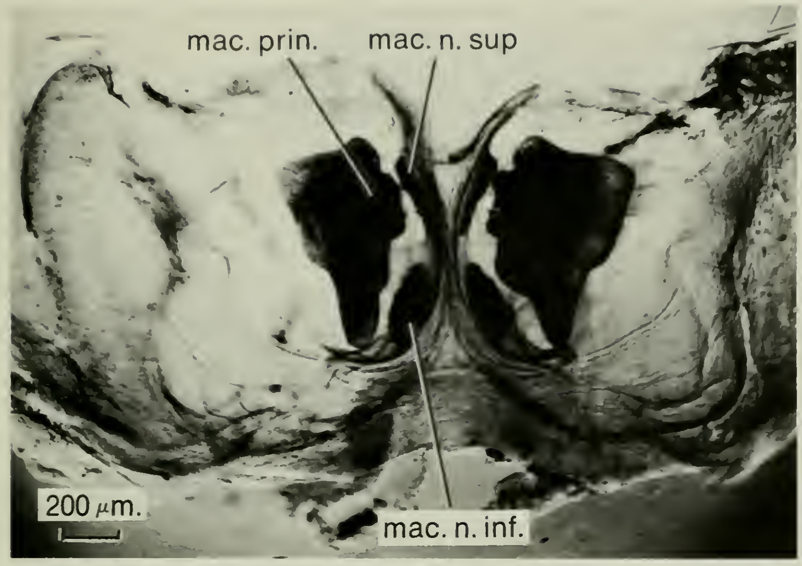

FIG. 6. The statocyst of the squid *Loligo*, as seen from in front. The calcium salts in the statoliths (the gravity stones) make them opaque. There is one very large one on each side, composed of crystals of aragonite. This stone lies in the transverse plane attached to sensory hairs of the macula princeps (mac. prin.). There are two other patches of sensory cells, carrying numerous small crystals. The macula neglecta superior (mac. n. sup.) lies nearly in the sagittal plane, the macula neglecta inferior (mac. n. inf.) in an oblique horizontal plane.

cisely the correct extent to hold the animal upright (fig. 7). If the statocysts are destroyed this is no longer possible. Notice, then, that the model serves to allow the action system of the animal to maintain its proper relation with the rest of the world—the essential feature of living.

For the detection of angular accelerations the cephalopods have ridges of sensory hairs, the cristae, carrying very light flaps, the cupulae. The cristae run along the sides of the statocyst sac in four directions, at right angles to each other (fig. 8). When the animal turns, the displacement of the wall relative to the fluid contents of the statocyst moves the cupula of one or more of the ridges according to the direction of movement. The signals set up by the hair cells of the crista thus represent the

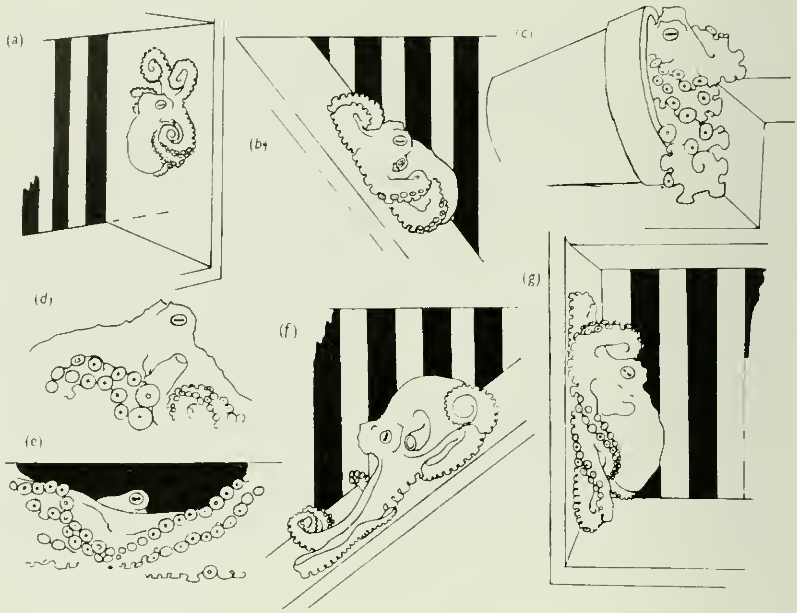

FIG. 7. Drawings by M.T. Wells to show how pupil of a normal octopus is always held horizontal (a-e). In f and g, are shown the positions of the pupils in an animal from which both statocysts had been removed.

animal's own movements. By their connections these nerve fibers then initiate compensatory movements, especially of the eye muscles.

This system is obviously similar to that of our own semicircular canals. It is indeed striking that in the more active cephalopods, such as the squids, the statocyst has become divided up and curved into shapes that in effect constitute actual canals. Our three semicircular canals serve to represent angular accelerations in three planes of space. What are the squids doing with *four* cristae? It may be that the answer is that with the fourth they detect linear acceleration forward or backward. These animals can move readily in these two directions, which is a feat not easily achieved even by their rivals the fishes. Budelmann (1975) has shown that the cristae are indeed capable of responding to linear acceleration (unlike the semicircular canals).

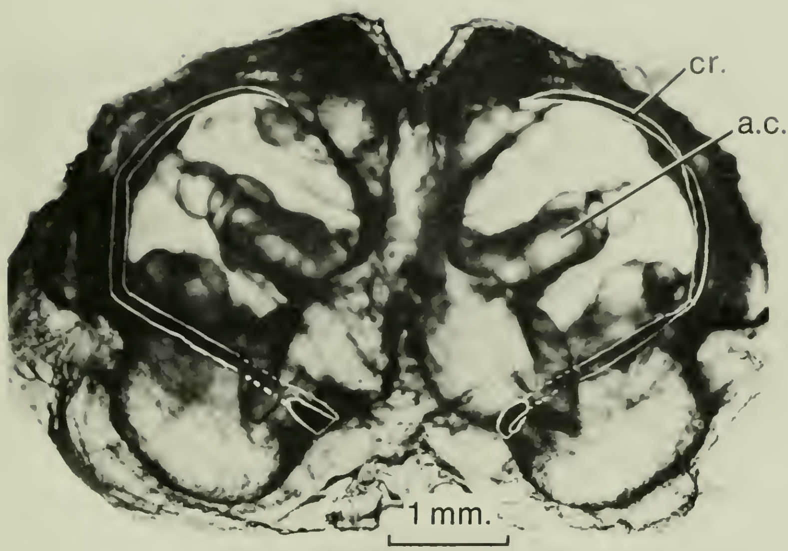

FIG. 8. Statocyst of the fast-moving squid *Loligo*, seen from above. The statoliths shown in figure 6 have been removed. The white outlines show the course of the crista (ridge) of sensory cells (cr) mainly for detecting angular accelerations. The ridge runs (on each side) across in front, along the side, across the back and then up in the vertical plane. The cavity has curved sides and is divided up by a number of projections (a.c.=anticristae). The effect is a restriction of fluid movement similar to that accomplished by the semicircular canals in vertebrates.

It is interesting to note that in octopuses and other cephalopods that do not make rapid turning movements the whole system is changed. The sac is very large and the anticristae are reduced or absent, leaving a single volume of fluid whose inertia gives greater sensitivity to slow movements (fig. 9). So in every animal the structure and connections of the sense organs have come to represent the environment in which it lives. Notice that the model that the animal contains represents not only the features of the world but also the actions that the animal must itself perform to keep alive. The models in the brain are not static pictures, they are the written plans and programs for action. In squids the giant cells that produce the jet lie very close indeed to the statocyst. If the animal is suddenly disturbed it immediately produces a jet. This plan of action does not have to

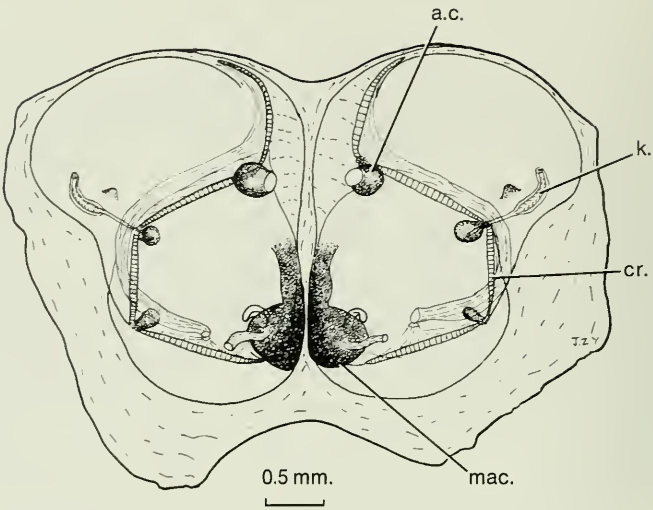

FIG. 9. The statocyst of the slow-moving squid *Taonius*, seen from above. The macula (mac.) and its stones are quite different from those of *Loligo*. The sac is large and the anticristae (a.c.) are small and few, so that the cavity is not divided up into "canals." K. is Kölliker's canal, a blind ciliated tube of unknown function; cr = crista.

be learned. It is written into the inherited wiring pattern.

In man and other vertebrates the cerebellum is a very important part of the system for control of movement. We have recently realized that there are lobes in the brains of cephalopods that contain large numbers of very small parallel fibers, strikingly like those of our own cerebellum (figs. 10, 11). We do not yet understand the full significance of these arrangements but a possible explanation is that the fine fibers serve to represent *time* (Braitenberg, 1967). They conduct very slowly and this may determine the braking action that terminates a movement. Many actions of the muscles are *ballistic*, in the sense that the ending of their contraction is determined when it begins and not by any feedback en route.

In ourselves the ear has the further function of detecting sound. Cephalopods seem to have no capacity for responding to vibrations, except those of very low frequency. This is very strange since water transmits vibrations that could have very

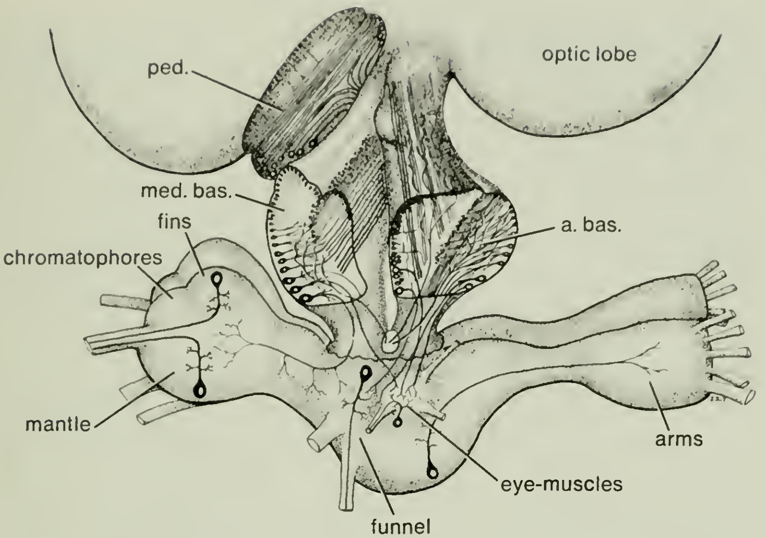

FIG. 10. A diagram of the brain of a squid showing the four sets of fine parallel fibers, somewhat similar to those in the vertebrate cerebellum. The suboesophageal lobes lie below and control the various movements as shown. The cerebellum-like lobes lie above them and are called the anterior basal (a.bas.), median basal (med. bas.) and peduncle lobes (ped.). The parallel fibers run in different planes; two sets are in the anterior basal lobe, one in each of the others. Notice that these lobes send fibers to the lower motor centers.

great symbolic value and indeed the fishes, great rivals of the cephalopods for domination of the waters, hear very well.

LEARNING SYMBOLIC VALUES

All the behavioral responses we have considered so far have been the consequence of connections laid down during development, but cephalopods are provided also with considerable powers of learning. Far less of course than in mammals or man but still enough to provide us with much information about the processes that are involved in memory formation. It is here that it becomes especially important to pay attention to our conceptual framework and language. The essence of learning is the attaching of symbolic value to signs from the outside world. Images on the retina are not eatable or dangerous. What the eye

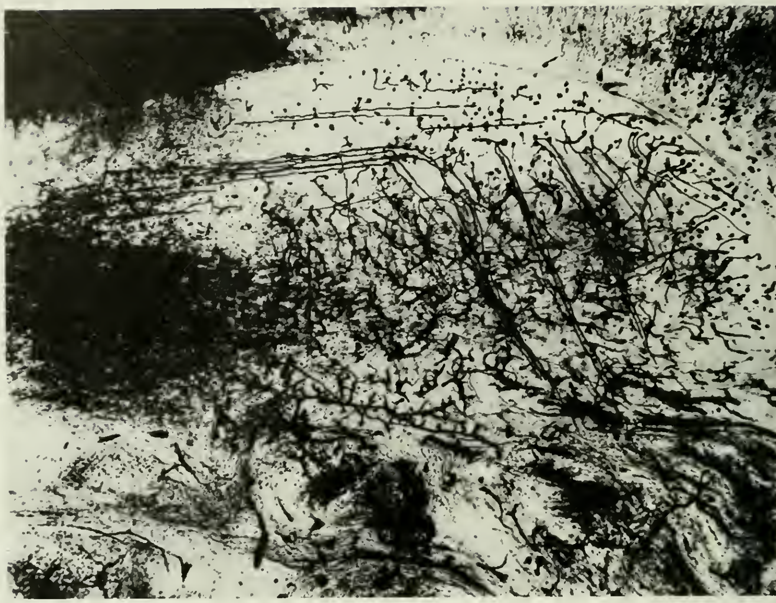

FIG. 11. Section of the peduncle lobe of a squid showing the fine parallel fibers. Stained by the Golgi method, which picks out a few fibers. The photograph has been retouched.

can provide is a tool by which, aided by a memory, the animal can learn the symbolic significance of events. The record of its past experiences then constitutes a program of behavior appropriate for the future.

Octopuses have two separate memory systems. One allows them to make appropriate responses to things that they see; the other does the same for the tactile and chemical properties of objects touched by the arms (fig. 12). These systems lie at the top of the hierarchy of nerve centers in the sense that they make the decisions as to which movements shall be executed by the lower parts. To revert to our military metaphor, they are the General Staff. They receive intelligence from the outside world and then write plans for programs of action by the whole army, in the light of their memory records of past experience.

With the visual system an octopus can learn to make attacks at one shape but to retreat from another. With the touch system

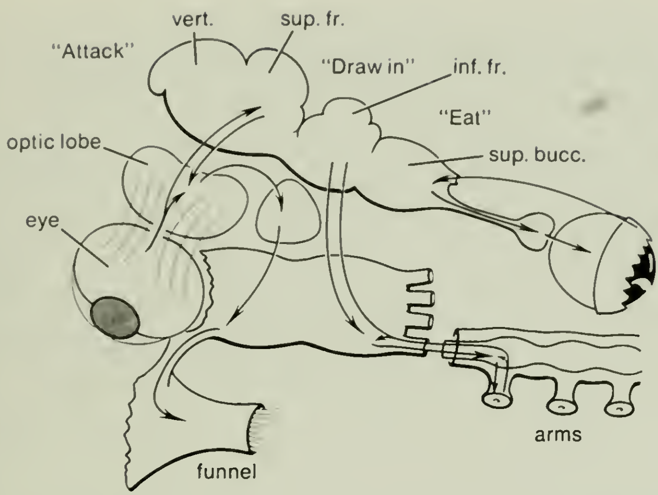

FIG. 12. Diagram of the brain of an octopus showing the parts that make up the two memory systems. The two are outgrowths from the superior buccal lobe, which controls the eating system (sup. bucc.). The inferior frontal system (inf. fr.) receives information from the arms and provides a memory regulating which objects are drawn in. The superior frontal (sup. fr.) and vertical (vert.) lobes are part of the visual memory, serving to decide which objects should be attacked for food.

he can learn to discriminate degrees of roughness and also chemical differences, detected by the suckers (Wells and Wells, 1956; Wells, 1963) (fig. 13).

The visual system has features again surprisingly like those of vertebrates in their principles of operation, in spite of great differences in detailed anatomy. We can see from these principles the stages that are necessary for the learning of symbolic significances by vision or touch.

FEATURE DETECTORS

The first essential is to have sensors that are competent to extract relevant information from the world. We know little about the physiology of these in cephalopods but something of their anatomy. There are cells with receptive fields in the outer parts of the optic lobes that seem suited to detect contours, as

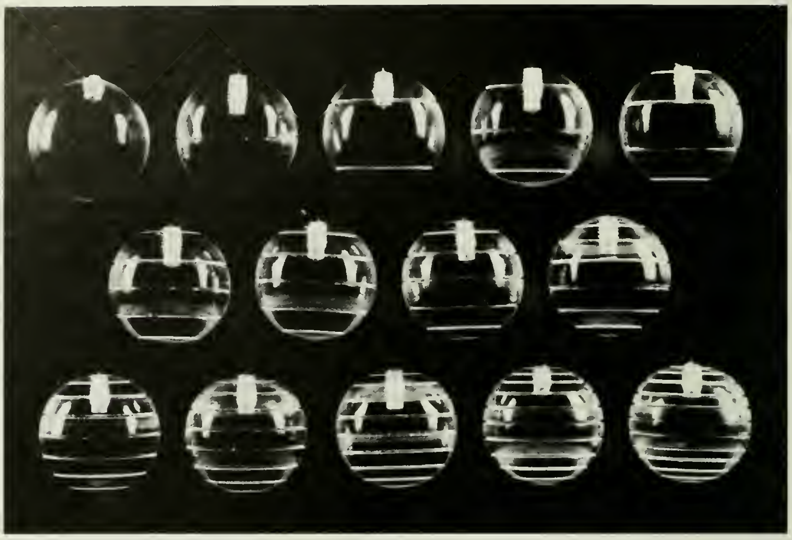

FIG. 13. Series of plastic spheres used for training octopuses to distinguish various degrees of roughness.

do cells of the visual cortex of mammals (fig. 14). Octopuses can be trained to react differentially to rectangles with vertical and horizontal orientations. It is probable that these features are detected by the receptive fields of these second-order visual cells, which seem to be tuned to receive signals from rows of optic nerve fibers. We note that such a system depends on a detailed somatotopic projection from the sensory surface of the eye. This presents a literal map of outside events, from which the brain then records certain features as it writes the programs that will determine its future actions. Moreover, these feature detectors lie in a layered system of neuronal processes, the plexiform layer, which is surprisingly like the layered structure of the vertebrate retina (fig. 15). Contributing to this layered neuropil are great numbers of amacrine and horizontal cells, with processes limited to the plexiform layer. Some extend over long distances, others are quite short, and we have as yet no information as to how any of them operate. Their presence, however, in essentially the same relations in cephalopods and

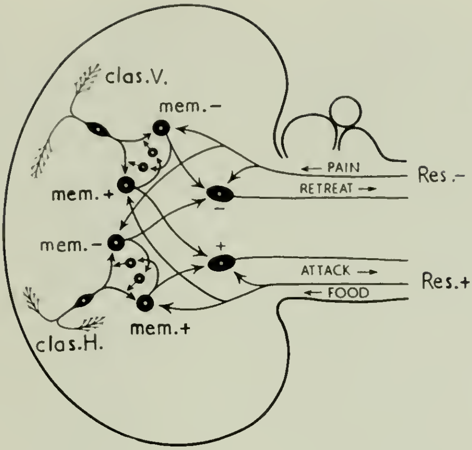

FIG. 14. Diagram of the optic lobe of an octopus to show the system by which it is suggested that visual contours are detected and memory records made that will control future behavior. Clas. V. and clas. H. are the "classifying cells," which respond to particular visual features (e.g., vertical or horizontal rectangles). The octopus can be trained to attack or avoid either of these, so the pathways from them msut lead to motor systems for attack and retreat. Following an attack the animal will receive either food or pain. The suggestion is that signals from the lips (food) or from the body (pain), besides promoting attack or retreat, will activate the small cells, which produce an inhibitory transmitter and block the unwanted pathway, leading to greater use of that which is "correct." The memory cells (mem.) only discharge if they receive signals both from the classifying cells and from the indicators of results (Res.+ and Res.-). The system is shown biased as it would be if the horizontal rectangle had been given food and the vertical shocks.

vertebrates should surely help us to find the principles that are involved in the extraction of significant visual features. Pribram (1971) has suggested that such systems recall the logical organizations necessary for encoding by and/or gates. We can also surmise from the work of Dowling and Werblin (1969) on the retina of the mud-puppy (*Necturus*) that these elaborate networks operate essentially as analogue computers, using patterns of graded electrical signals to compute from the patterns that are sent to them from the retinal receptors suitable all-or-none signals to pass on to the next stage in the brain.

Unfortunately, we know rather little about how to pursue such signals, either in cephalopods or vertebrates, to the points

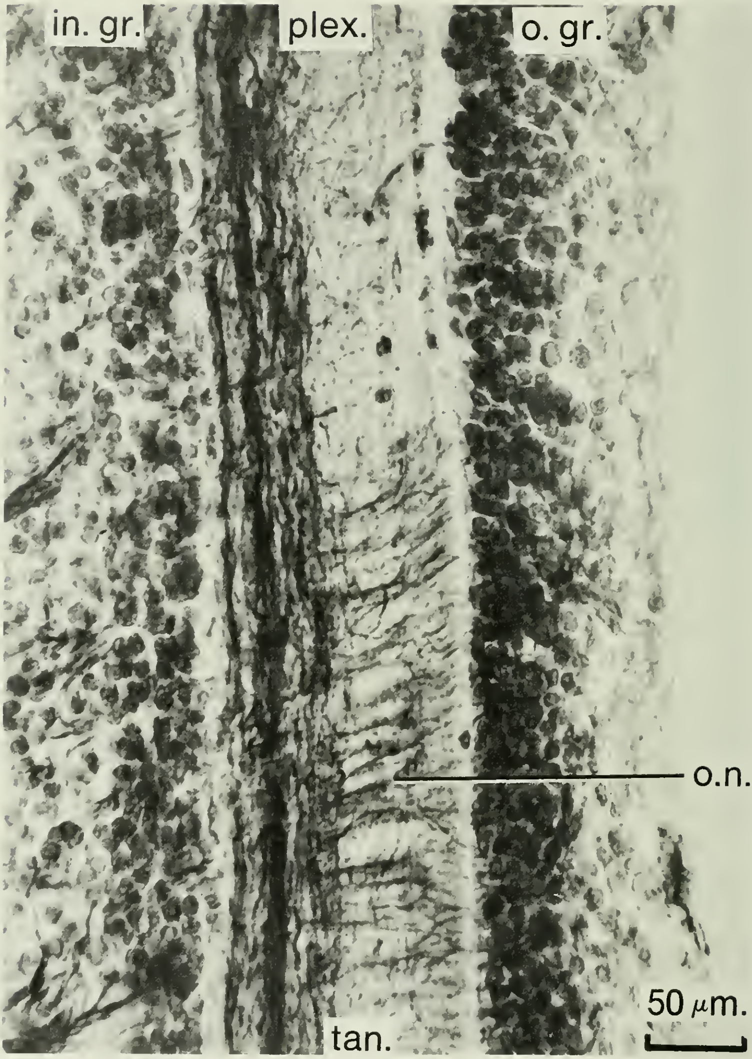

FIG. 15. Photograph of a section of the surface of the optic lobe of an octopus, showing how it resembles the vertebrate retina. There are outer and inner granule cell layers (o. gr. and in. gr.), with a plexiform layer between (plex.). The optic nerve fibers come in from the right (o.n.). They have disappeared from the upper part of the figure where some of them had been cut some days previously. The inner tangential bands of fibers in the plexiform zone (tan.) are the receiving dendrites of the "classifying cells" shown in figure 14. They have remained intact. Cajal's silver stain.

at which the changes occur that constitute the writing of a new action program by the memory mechanism. In squids we can say that there are only one or two further synapses between the feature detectors and the giant cells. Therefore, although the optic lobes are indeed large and complex, there is no need to suppose that any very elaborate system of operations has to intervene between detection and behavior, even in learned behavior.

However, somewhere in this pathway there must be the possibility of an alteration in connection patterns, if that is the mechanism by which the memory system works. I have suggested that this is done by the operation of a switch system that reduces the probability of using one pathway in favor of the other (fig. 14). It may be that once one path begins to be used rather than the other there will also be a subsequent increase in its availability, perhaps by added synaptic connections or efficacy, as has been suggested, following Cajal (1895, see 1953 p. 887), by many workers (e.g., Hebb, 1949; Young, 1950). But whatever mechanism is used to establish the symbolic value of some set of nervous signals, it must involve a *reduction* of the number of possible behavioral responses. The octopus can originally react either positively or negatively to a horizontal rectangle; his experience restricts him to only one of these responses. A given signal cannot symbolize *both* something good and bad. I have suggested that the switching of each single neuronal pathway constitutes a unit of memory or mnemon. It is the single "word" of the writing that constitutes the new program of action. The octopus is a very simple creature and perhaps it learns only single words. We have to learn not only words but whole "sentences," indeed whole "books," which constitute the action programs that become written in our memories.

For the establishment of symbolic value it is essential that the results of action can be referred to a standard, which must ultimately be set by the genetic composition, the historical information encoded in the DNA. Such signals of the results of action come from the taste systems on the one hand and the pain systems, producing aversive responses, on the other. We do not know much about them in octopuses but there is evidence that if they are prevented from reaching to the appropriate parts of the brain no learning is possible. We notice that these nerve impulses, like all others, are symbolic, in this case symbolizing internal states that are either satisfactory or unsatisfactory for life. The symbolic value is established by the long sequence of selections that have produced appropriate DNA. Those organisms that do not have an appropriate taste for food and life or skill in avoiding pain do not survive.

The anatomy suggests that in the octopus, as in vertebrates, special patterns of connection are used to allow these reference signals to meet with those coming from the outside world. In both the visual and touch memory systems of the octopus there are lobes in which this interaction can take place (fig. 16). The

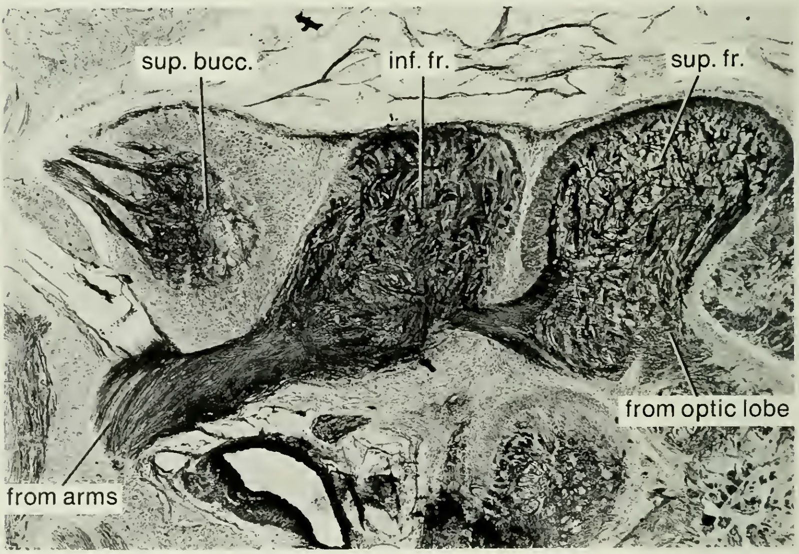

FIG. 16. Photograph of sagittal section through the front part of the brain of an octopus, showing the inferior frontal (inf. fr.), superior frontal (sup. fr.) lobes, and superior buccal lobe (sup. bucc.). These serve to mix signals of taste (from the lips) with those from the arms and optic lobes (respectively). The two lobes have similar structures, with many interweaving bundles, allowing for the mixing. Cajal's silver stain.

output of the lobes in both cases passes through a further lobe consisting of large numbers of very small cells, the vertical or subfrontal lobes (fig. 17). Many lines of investigation have shown that these lobes are involved in the process of recording in the memory, but are not absolutely essential for it. Their action seems to be particularly in restraining the animals from performing actions that are likely to be damaging. The numerous minute cells in these lobes can be seen with the electron microscope to be packed with synaptic vesicles (fig. 18). How they operate remains a very interesting question.

In general we can say that if learning consists in increasing the probability of performing certain "correct" actions when symbols appear, then it is necessary to have inhibitory systems to restrain the performance of other actions. A multichannel system such as this operates by means of a maximum amplitude filter in which many elements may be active but only the *most* active takes control (Taylor, 1964). It is suggested that the cerebral cortex contains systems that act in this way. Perhaps the prefrontal lobes in particular have a restraining influence in

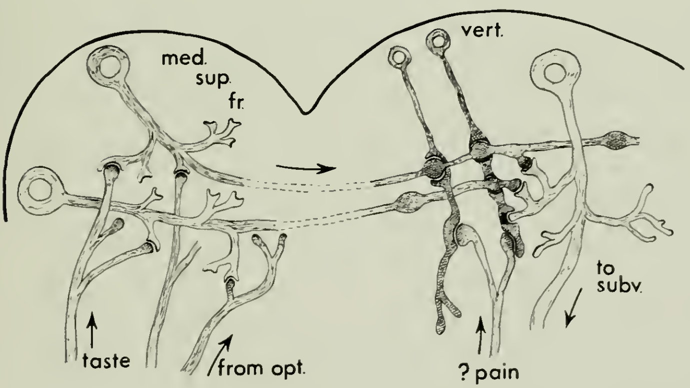

FIG. 17. Diagram of some connections of the median superior frontal (med. sup. fr.) and vertical lobes (vert.) of an octopus as shown by electronmicroscopy. The short amacrine cells in the vertical lobes are packed with synaptic vesicles. They are influenced by the fibers from the superior frontal and also by those entering from below and probably signalling pain. They influence larger cells leading to the subvertical lobe (subv.) and so back to the optic lobes (opt.).

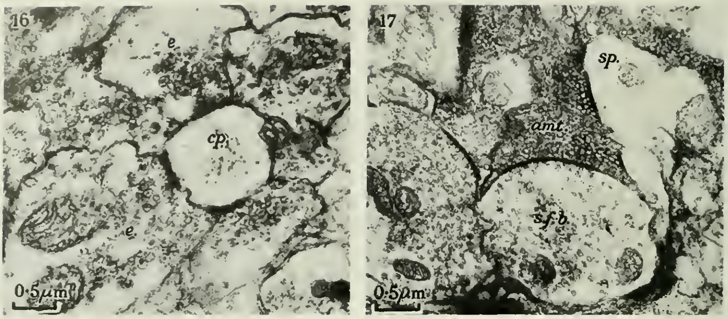

FIG. 18. Electronmicrographs of synaptic contents in the superior frontal (on right) and vertical (left) lobes of an octopus. The synapses in the former are between incoming fibers (e) and cell processes (cp.). In the vertical lobe the amacrine trunks (amt.) receive synapses from the axons of the superior frontal (s.f.b.) and transmit to spines (sp.) of cells that carry signals away from the lobe.

man, allowing the performance of such delicately graded actions as those of effective speech in a social context.

Human brains, like those of octopuses, must contain reference systems to determine which lines of action are likely to be successful in maintaining life. We can indeed begin to see some evidence that they operate in ways rather like those described. Ungerstedt (1971) and others have shown that there are systems of aminergic pathways leading upward from centers in the medulla to the hypothalamus and on to the limbic system and frontal cortex (fig. 19). These pathways, such as that beginning in the nucleus coeruleus, come from regions where fibers from the taste buds enter the brain. Crow and his colleagues have produced evidence that rats with lesions to this pathway cannot learn to run a maze for food reward (Anlezark, Crow, and Greenaway, 1973). Moreover, with electrodes implanted in these regions animals will press repeatedly for self-stimulation. There are controversies about these experiments, but it seems very probable that we are approaching here close to the core of many problems that have worried mankind for centuries, and do so still. The reference signals that come from these pathways, and from the hypothalamus, provide the aims and objectives of our lives and the course of our learning. Of course crude

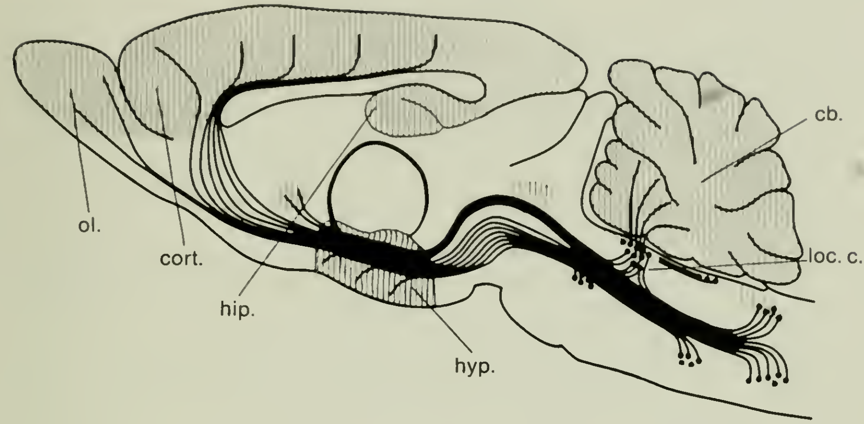

FIG. 19. Diagram of the ascending pathways on the rat's brain that use the transmitter noradrenaline. They begin in the locus coeruleus (loc. c.) and other centers in the hind brain. From here they ascend to the cerebellum (cb.), hypothalamus (hyp.) and finally reach to the cerebral cortex (cort.), olfactory bulb (ol.) and hippocampus (hip.). The terminal areas are shaded (after Ungerstedt, 1971).

rewards do not necessarily enter into every associational act, especially in man. We have acquired more subtle systems of reward to supplement those of taste and pain. Nevertheless, we begin to see how life depends upon symbolic signs of life values, which are used to give symbolic significance to the signals we receive from the outside world.

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