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Published by: American Academy of Arts & Sciences
Stable URL: http://www.jstor.org/stable/3823436
Accessed: 05/08/2009 15:16

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Vision and the Brain

At the January Stated Meeting David H. Hubel, George Packer Berry Professor of Neurobiology at the Harvard Medical School, presented the following account of his research, undertaken in collaboration with Dr. Torsten Wiesel, on the visual system of higher mammals.

The statement that the brain is a very complicated structure is so obvious as to seem a truism. But as an introduction to a discussion of specific aspects of the brain, it is useful to examine the basis for this assumption of great complexity. First, since we believe that the brain is responsible for what we do and think and perceive, and since we regard those functions as very complicated, we naturally conclude that the organ responsible for them is likewise complicated. Another source of this assumption is the large number of cells which, anatomists tell us, the brain contains. The usual estimate is $10^{10}$; however, it has even been said that the cortex itself contains $10^{11}$ cells, which gives an indication of the degree of confidence that one can place in such counts. But in any case very large numbers are involved, numbers that are, in fact, literally astronomical. On the other hand, if one were to count the number of cells in the liver, similar estimates would probably be put forward, and I am sure that not even the most devoted hepatic physiologist would try to claim that the liver is as complicated as the brain. Clearly other things besides mere numbers must be important in determining complexity. For one thing, the cells in the brain are interconnected in very complicated ways. Furthermore, the liver contains only one or two kinds of cells, and the cells of a given class work in parallel ways to perform the various functions of this organ — in medical school we were taught fifteen, but the list of the liver’s functions is probably now much longer. In the brain there are many kinds of cells — the number might be between one hundred and five hundred, depending on how finely one differentiates. They perform a large number of different functions.
I must emphasize at the beginning that our knowledge of the brain is in a very primitive state. While for some regions we have developed some kind of functional concept, there are others, the size of one's fist, of which it can almost be said that we are in the same state of knowledge as we were with regard to the heart before we realized that it pumped blood. The frontal lobes would fall into that category.

My topic deals with a few parts of the brain—the visual areas—that we are beginning to understand in a preliminary way, although we are still far from being able to say with any precision that we know how one sees. One reason why our knowledge in this area is at this primitive level is that until recently the elements of the subject simply were not available. In order to understand how the brain works, we needed some understanding of its constituent elements. It is only in the last twenty years, by virtue of the work of people such as Hodgkin, Huxley, Katz, Kuffler, and Eccles, that we have learned how single cells work in the brain. In order to make my subsequent remarks more intelligible, I want to describe briefly the nature of nerve cells and nerve impulses as elucidated by this recent research.

A typical cell in biology is a glob of protoplasm surrounded by a membrane. The nerve cell, however, looks very different from other cells; it is extremely deformed and contorted. Nevertheless it is protoplasm surrounded by a membrane, and the cell body is analogous to that of any other cell, with its nucleus and various housekeeping organs. In addition, the nerve cell has parts that are specialized in various ways. One part is called the axon or nerve fiber, the terminals of which transmit signals to the next cells. The cell body is ordinarily about a fiftieth of a millimeter in diameter while the length of the axon averages a millimeter or so, but in some kinds of nerve cells it reaches enormous lengths—up to several meters. The parts of the cell that receive signals from other nerve fibers are called dendrites. Electrical signals travel down the axon from the cell body to the terminals. Across the membrane of a nerve cell there is an electrical
charge of about a tenth of a volt, positive outside and negative inside. When an electrical signal occurs, this charge reverses for a short length of time, about a thousandth of a second, so that it becomes positive inside and negative outside. This reversal sweeps down along the axon and recovers very quickly, so that at any given moment there is occurring the reversal and behind it a re-reversal back to the normal state of affairs. The impulses are all the same size and shape, and they always move in the same direction in any given nerve cell; they vary only in their frequency. The cell fires more or less rapidly, with more or fewer impulses per second, depending on the information transmitted from other nerve cells. This signal travels to the terminals where, before it dies out, a chemical is released that diffuses to the membrane of the next cell and affects it so as to increase or decrease its rate of firing. Thus, the numerous contacts between cells may be excitatory or inhibitory. How fast any given cell fires depends on the sum average of the thousands of endings from all the nerve cells that make contact with it. The more active the excitatory inputs, the faster the cell fires; the less active the inhibitory endings, the faster it fires. And conversely, the less the excitation and the more the inhibition, the slower the firing. If the inhibition is great enough, the cell will stop firing completely.

This brief sketch gives a taste of some of the biophysical work of the past twenty years. At the present time, our knowledge of how nerve impulses and nerve interconnections work is reasonably good. As a result of this one-cell-level research, scientists have been able for the first time to start examining larger units of the nervous system. Although we have known for a long time how these things fit together anatomically, the interpretation of their interrelations has been very difficult because we had no knowledge, for instance, of the very existence of inhibition. Certainly major gaps still exist, but we have enough understanding to begin to examine how these elements are assembled to make up the nervous system.

We can view the functioning of the nervous
system as a huge circuit of interconnected cells between an input and an output. Each neuron or nerve cell is affected by many cells and can affect many cells. At the first stage of this process is a specialized kind of cell called a receptor, the electrical signals of which are influenced not by other nerves ending on it but by information from the outside world; the receptors in the visual system are influenced by light. There are approximately 125 million receptors in each retina, and these influence by their electrical signals a set of ordinary neurons also located in the retina. Each of these nerve cells receives input from many receptors, and the axon that it sends out is in turn capable of influencing many cells in the next stage. The process goes on and on, in stage after stage, first in the retina where there are roughly three such stages, and then in the brain. Cells receive input and furnish input to subsequent stages, until finally we reach a class of cells the nerve fibers of which end on muscle cells. This forms the final output of the nervous system. Without an input one is cut off from what is going on in the world; without an output one has no influence on what goes on in the world. It is the combination of these two elements that, we might say, defines an animal. This is, of course, an oversimplification of the operation of the nervous system. There are circuits that go backwards for a while, for example, and many banks of receptors for different sensory modalities, many different kinds of muscles, and all kinds of highways and byways. The brain viewed anatomically is a very baroque instrument. But this at least provides a framework to build on; the major direction of signals is from the input towards the output, even though delays along the way are not uncommon.

One strategy for understanding the nervous system involves the study of sensory stimulation. We can stimulate an animal by shining light on its retina, for example, or sending sounds into its ear; and if we insert a tiny wire close to a given cell and listen to the signals that the cell emits, we can discover what kinds of stimuli cause that cell to fire more or less rapidly. After studying
many nerve cells at a particular stage and having reached some conclusions as to their common features, we can move on to the next stage. By comparing one stage with the next, we can advance some conclusions about the function of this complicated anatomy, conclusions that probably could not have been derived by studying the structure without listening to the signals. For the past twenty years Torsten Wiesel and I have been carrying on studies of this sort on the visual system of higher mammals, mostly cats and monkeys, and in this time we have reached about the sixth or seventh stage from the receptor cells. I shall describe some of the ways in which the higher mammalian visual system works at these early stages, but I must emphasize that our conclusions by no means solve the main question in vision— that is, how the brain makes sense of the image that falls on the retina, the image of a scene rich in form, color, depth, and movement. We are only beginning to see a few steps along the way, but it is encouraging to discover that at the early stages at least a rational process is in operation. There does not seem to be any magic or mystery involved to impede understanding, and we can assume with some confidence that the whole brain will be comprehensible through rational methods.

In the mammalian brain the array of receptors and the first two stages of neurons in the visual system are housed in the retina. The axons coming from the third stage combine to form a large bundle, the optic nerve; these fibers pass uninterrupted to a nest of cells deep in the substance of the brain called the lateral geniculate bodies, and most of these cells in turn send their axons out through the substance of the brain to a part called the primary visual cortex. In this region of the brain there are four or more stages. Thus, roughly speaking, stages one to three are in the retina, stage four in the geniculate, and stages five to eight in the cortex. The cells at the more advanced stages send their output either out of this part of the cortex to various neighboring cortical regions, or down to several structures in the depths of the brain. Our anatomical knowl-
edge of stages subsequent to the cortex is extremely vague, and this discussion will deal primarily with what happens up to and including the primary visual cortex.

At the optic nerve and the lateral geniculate levels the cells function in a roughly similar manner. In cells at both levels the kind of stimulus that elicits a response is basically a small spot of light placed in a certain part of the animal's visual world. If you shine a spot of light larger than the area that activates the cell, the response becomes very much weaker. It turns out that in making the spot larger you have covered another region which is feeding into the cell and is inhibitory to it. If you shine light both on the inner part and the outer part simultaneously, you are in effect telling the cell to fire slower and faster at the same time, and the cell's tendency is to ignore the stimulus. Usually the center wins out over the surround, so that a large spot tends to excite the cell but more weakly than a small spot would. The cell responds vigorously, though not quite optimally, to many other kinds of stimuli besides round spots—for example, with a long narrow slit of light, where one is stimulating all of the center part and only a fraction of the surround, the center wins out strongly, and the cell tends to respond very well. There is one technical detail to add to this: if the stimulus is confined to the surround the cell fires more slowly; when the stimulus is eliminated, the cell often gives a brisk discharge—it fires much faster than it does spontaneously, as though to make up for lost time. The explanation for the phenomenon called "off discharge" is not completely known, but the responses are often useful to the neurophysiologist: when a cell has a very low spontaneous firing rate, the off discharge may provide the first hint that the area stimulated is inhibitory.

At first we might wonder why nature would develop such a strange format for the operation of the optic nerves. On reflection, however, we realize that the center-surround organization with inhibition from the surround indicates that the cells are making a spatial comparison between the
amount of light in the central region and the amount of light in the immediate surround, and such comparisons are in fact one of the basic functions of our visual system. Absolute values of light are not of much interest to us in our daily lives. The appearance of something, whether it is light or dark, depends very little on the amount of light coming from it; it is the comparison between the object and its surround that is important. A television tube when the set is turned off looks white or grayish; when it is on, the tube can only be brighter than it is when it is turned off, and yet many areas appear richly black in contrast with other lighter images.

In the cortex the cells operate in a very different way from cells at any previous stage. There are two major differences. First, optic nerve fibers and the lateral geniculate cells are influenced only by one eye. The geniculate is partitioned into regions, some of which receive their input from one eye, some from the other; the individual cells are all monocular. It is in the cortex that for the first time one finds cells that are influenced by both eyes. Second, the cortex takes information from the eyes and rearranges it in a special way so that most of the cortical cells are stimulated not by spots but by straight-line segments. Each individual cell responds best to a short length of line in a particular small part of the visual world, and that line must be tilted at a certain angle. If you shine the line anywhere else in the visual world of the animal or if it is tilted at a different angle, the cortical cell being examined will not respond. Some cells respond if the line is swept across the region of interest in both directions; others are more selective and respond only to one direction and not to the diametrically opposite direction. The line segment can be produced in a number of ways: it can be a dark line on a light background, a light line on a dark background, or an edge boundary between dark and light. In the case of a slit or dark bar, if the line is thick enough to cover the entire region, there is no response; excitation and inhibition completely cancel each other. Thus, the cell does not respond
if a flashlight is directed into the eye of the animal. This seems to be a useful arrangement, because such a stimulus does not contain much information, and it would be inefficient if it were to tie up the activity of all the cells in the cortex. Cells in this part of the cortex can be grouped into several (at least four) different grades in terms of the complexity of their responses. Simplest of all are the cells that get their input directly from the geniculate: these in fact respond very much like geniculate or retinal cells, without specific sensitivity to lines. Cells in the other three classes—the great majority—all have line-orientation specificity.

If we close one eye of an animal and, by stimulating the open eye, work out the properties of a binocular cell in the primary visual cortex, identifying the receptive field and the best orientation of the stimulus, and then do the same with the other eye, we find that the receptive field and orientation are exactly the same relative to where the animal is looking. If there is any directional selectivity, that is also the same in the two eyes. Every response of the right eye is imitated by the left eye—the complicated and intricate connections that the cell gets from the left eye are duplicated at least qualitatively by a similar set of connections from the right eye. Since one sees this phenomenon in newborn monkeys, it clearly does not come about by a process of learning. It is the result of a wiring that is part of our inheritance, just as the anatomy of our knee joint is.

Moving from one cell to the next in the cortex we find cells that cover all orientations for all parts of the visual field. The optimal stimuli can be exceedingly small. For any given region of the animal's visual world there are many cells representing all orientations. If one objects that such an arrangement calls for many millions of cells, the answer is that the brain has just that. Cells seem to be cheap, biologically, and the brain does things in ways that no engineer would even consider.

What are the conclusions to be drawn from this knowledge? First, it is clear that a very efficient system is in operation. If the stimulus is,
for example, a dark glob on a light background, any cell whose territory of concern is within that form will not be influenced by its presence or absence because these cells are not influenced by overall illumination of their receptive regions. However, a cell whose receptive field is cut by any part of the border will respond provided it happens to be interested in line segments that go in the direction of the border at that point, but not otherwise. Thus for every small region along the border of the dark patch a few cells will be strongly influenced and will fire rapidly. A stimulus will therefore not necessarily occupy many cells, as long as the form is relatively simple. Secondly, we are led to conclude that at this early phase in perception, a scene is analyzed in terms of its dark-light contours by determining the way the contours run at every point. The cells are detectors of direction at any point along a line or a curve. (It is a mistake to think of them as “line detectors.” A curve will influence a cell as well as a line, provided the receptive field of the cell is small enough so that within that receptive field the curve is sufficiently straight to produce a response.) Of course, this knowledge by no means tells us how we recognize a hat or a boat or a face. The information from cells at this stage is fed on to subsequent stages, and at some point sense must be made of it. We have no idea of how that is done. But at least we know that up to this point the system works in a rational way that can be understood. Curiously, as far as I know, no one predicted that the initial stages of form analysis would use such a strategy.

Beyond the primary visual cortex we know very little. In the next area, the cells seem to be concerned with binocular depth. They compare the two images on the retinas and from that comparison come to some conclusion about the eyes’ distance from an object. Areas still further along seem to be preoccupied with the analysis of colored stimuli.

Now let us look at how the primary visual cortex is built up. Our original impression of the structure of this piece of machinery has been changed significantly by a better understanding
of both its physiology and its anatomy. The cortex is a plate of cells which in man is about a foot and a half in square area and about two millimeters thick. It is a very bizarrely shaped structure, richly folded and creased. Below each square millimeter of surface there are on the order of a hundred thousand cells. In the cortex, neighboring cells very often have the same characteristics, and this leads to a complicated but in places rather beautifully patterned geometry. The fibers from the lateral geniculate, the input to the cortex, make their contacts with the simplest cortical cells; these, as mentioned above, show no selective responses to different line orientations. Moreover, unlike the cortical cells in more advanced stages, they almost invariably respond only to one eye, and two neighboring cells almost always respond to the same eye. If a microelectrode is pushed along this layer of cells, recording from cell after cell, we find that for about a half a millimeter all cells respond to the same eye; then there is a sudden switch, and all cells respond to the other eye.

Until recently the pattern of these left-eye, right-eye regions was unknown. Such an array of patches could result from a checkerboard-like arrangement or an arrangement in parallel stripes or a series of islands of left-eye embedded in a sea of right-eye— all, when cut in cross section, would show the left-eye, right-eye sequence. About five years ago we developed a method that elucidated the pattern anatomically. Without going into detail let me simply say that we injected an amino acid into one of the eyes, which was absorbed by the cells in that eye and then shipped down the optic nerve to the geniculate and from there to the cortex. We could then stain the cortex selectively and identify the regions that corresponded to the injected eye. These stained regions were separated by unstained regions corresponding to the other eye—a clear anatomical verification of what we knew physiologically. The power of this method is that it allowed us to cut through the cortical region in question and see what it looked like en face. The areas corresponding to the injected eye are in fact parallel
stripes separated by regions that correspond to the other eye. Just as with fingerprints, the details vary from animal to animal and even in the two hemispheres of the same animal. In different individuals of the same monkey species, for example, the general plan is similar, but the details are different: two stripes belonging to the same eye will sometimes adjoin, with the intermediate stripe from the other eye ending blindly.

In this same piece of cortex another structure was identified which was also unknown before these techniques were developed. Looking now not at which eye elicits a response but at what is the best orientation of the stimulus, we find a distinct plan in the way that these orientations vary from cell to cell. There is in fact a progression of orientation. If we advance an electrode a few thousandths of a millimeter from one cell to another, the orientation of the second is almost the same as the first but tilted slightly farther. As we advance still farther, the angle of tilt continues to increase. The orientation may in this way proceed by small steps all around the clock several times. Here and there, for no obvious reason, there may be reversals of the progression, with a change from clockwise to counterclockwise and back. If, on the other hand, one makes a penetration exactly perpendicular to the surface, the orientation stays constant. Thus one has the impression of the cortex being organized into a series of very fine orderly vertical columns in each of which the orientation is constant. A few years ago a method was discovered that could show this anatomically. Again to gloss over unnecessary details, a certain kind of sugar is injected into the bloodstream of the animal so that it is available to all of the cells of the animal including the brain cells. The more active any cell is in the body, the more sugar it consumes. After being injected with the sugar, the animal is stimulated in a particular way, and then the area of interest in the brain is stained for that sugar. In one experiment we stimulated the entire visual field of the animal with vertical stripes for three-quarters of an hour. When we cut the brain

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in cross section, we could see the regions of constant orientation that are indeed the regions in which the cells respond to vertical. They are separated by unstained regions in which the cells presumably respond to horizontal or oblique. One concludes, then, that there are in the primary visual cortex two coexisting sets of slabs subserving entirely different things, one concerned with eye dominance, and the other with orientation. At the present time this is the extent of our knowledge of this particular area of cortex, which in the human occupies only about 5 percent of the total cortex. For the many other regions, all with their separate duties, not even this preliminary knowledge is presently available.

Thus we are led to expect that each region of the central nervous system has its own special problems that require different solutions. In vision we are concerned with contours and directions and depth. With the auditory system, on the other hand, we can anticipate a galaxy of problems relating to temporal interactions of sounds of different frequencies, and it is difficult to imagine that the same neural apparatus deals with all of these phenomena. Whereas in the case of molecular biology the impressive accomplishments of the past twenty years or so have enabled us to understand something about life in a very profound way, in the nervous system, I believe, we cannot expect this kind of general solution. Rather, we will have to go from one problem to the next, solving each separately. Perhaps in a few cases, such as memory, the answer may be some relatively simple biophysical trick that the cells play which may not involve complicated circuits. But for the major aspects of the brain's operation no master solution is likely; our understanding of the neural apparatus will most likely advance step by step as new techniques make it possible to solve individual problems. We are only at the beginning of this process, and we can therefore look forward to many such pleasures of discovery in the future.

David H. Hubel