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TRANSFORMATION OF INFORMATION IN THE CAT'S VISUAL SYSTEM

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When we look at an object, the image on our retinas has an effect on millions of receptors. The spatial and temporal patterns of excitation in these rods and cones represent raw information that must be handled by our central nervous system if we are to perceive the object in depth and color, and recognize it regardless of exactly where on the retina its image happens to fall.

In this paper I shall describe some of the results that Torsten Wiesel and I have obtained over the last five years in the course of a study on the visual systems of cats and monkeys. We have tried to learn something of how the brain deals with visual information by recording from single cells at several different stages in the pathway from retina to cortex, examinins the responses of cells to retinal stimulation at each stage.

Our recording and stimulating methods are relatively simple. The animal is anesthetized and its head is held firmly in a stereotaxic head holder. We introduce a metal electrode —usually a fine wire insulated almost to the tip—into some part of the visual pathway, until it comes close enough to a single cell or fiber to sample the currents associated with all-or-none impulses. We try to keep the electrode outside the cell so as to avoid injury to the membrane, since injury tends to distort the normal firing patterns. The eyes are held open, and to prevent eye movements we paralyze the eye muscles with a neuromuscular blocking agent. The animal faces a wide screen several meters away, on which we project spots or patterns of light. To keep the corneas from drying out we put contact lenses over the eyes, and we usually have to fit the cat or monkey with a pair of refracting lenses, to be sure that the pattern on the screen is focused on the retina. For each cell examined we try to find the most effective stimulus by varying the position, shape, color, and possibly the rate of movement of the image.

In this type of study one ought ideally to begin by recording from the receptors themselves, the rods and cones of the retina. One would then do the same for the bipolar cells, and so proceed step by step along the visual pathway, comparing each stage with the preceding one. Unfortunately, making single-cell records from the first two stages turns out to be technically very difficult, so that at present very little is known about the physiology of receptors or bipolar cells. While this would seem to be a bad start toward understanding the visual system, there is the consolation that one can record from cells at the next stage, the retinal ganglion cells. By studying responses of these one can tell how information has been transformed over two sets of synapses, even if one cannot identify the individual steps.

The results of stimulating mammalian retinal ganglion cells by shining small spots of light on the retina were first described by Kuffler in 1953. He found, as did others

fall into two large categories, which we have come to term 'simple' and 'complex'. Simple cells have the property that their receptive fields can be divided into excitatory and inhibitory regions. They differ one from another in the details of distribution of these regions, but have one thing in common: that areas giving excitation and inhibition are not separated by circles, as in the retina and geniculate, but by straight lines. Some cells, for example, have receptive fields with a long narrow excitatory area, flanked on either side by inhibitory areas, whereas others have the reverse arrangement, an inhibitory area flanked on the two sides by excitatory areas (Fig. 1, C and D). Some fields, like type G of Fig. 1, have only two regions of opposite type separated by *a*. single straight line. Summation occurs just as it does in the retina and geniculate, and the most effective stationary stimulus for a cortical cell is one falling on either the excitatory parts of a receptive field or the inhibitory parts, but not on both simultaneously. Consequently, stimuli such as long narrow rectangles of light ('slits'), or dark rectangles ('dark bars'), or straight-line boundaries with light to one side and darkness to the other ('edges'), are likely to be the most potent stimuli for cortical cells. Moreover, the stimulus that works best in influencing a cell, exciting or inhibiting it, will do so only when shone on the appropriate part of the retina and in the correct orientation. Some cells prefer one inclination, vertical, horizontal, or oblique, others prefer another, and we have no reason to think that any one inclination is represented more often than another. We call the inclination of the most effective stimulus the 'receptive-field axis orientation'. This seems to be one of the cell's most important characteristics. For example, if we record from a cell with a field of type C (Fig. 1), and shine a long narrow slit of light with just the right shape and in just the proper position and orientation to cover the excitatory area (marked by x's), we evoke an optimum response. Changing the orientation by as little as 10-15° will greatly reduce the response, and if the stimulus is shone at 90° to the optimum orientation, there is as a rule no response at all (see Hubel and Wiesel, 1959, Figs. 2 and 3). It is not hard to see the reason for this; a slit oriented in any direction but that of the field axis will illuminate excitatory and inhibitory areas at the same time, and the effects will tend to cancel. Of course even if the slit is properly oriented for this cell, it will not exert its maximum effect unless it is positioned exactly over the excitatory area, because otherwise it either straddles opposing areas or else covers only a small part of the total excitatory area. As we shall see, complex cells, unlike simple ones, are not so concerned about the exact position of the stimulus, as long as the orientation is correct.

Simple cortical cells, and for that matter complex ones too, have another important property. I have already mentioned that for a retinal ganglion cell, and even more for a geniculate cell, diffuse light is far from an ideal stimulus. As a rule it evokes a response, but a much weaker one than that produced by a centred circular spot of just the right size. This discrimination against diffuse light is apparently a progressive process as one proceeds centrally along the visual pathway, for with cortical cells there is generally no response to diffuse light, or at best only a very weak one. Here it is as though the excitatory and inhibitory parts of the receptive field balanced almost perfectly. This is a most astounding thing: after five years we are still amazed each time we record from the striate cortex, to find that a cell which reacts so vigorously to a very special stimulus does little or nothing when a bright flashlight is shone right into the eyes. Perhaps this is because it is so natural to assume that the best stimulus for a cell in the visual system should be one that affects every receptor in the retina. It is hard to swallow the notion that it is exactly the worst!

Here the neurophysiologists may ask why a diffuse flash of light evokes a cortical slow wave, if only a small proportion of cells respond to the stimulus, and these only relatively weakly. While too little is known about slow waves to permit an entirely

satisfactory answer, it is possible that detectable waves may be produced by relatively few cells reacting weakly but synchronously. It is worth noting in this connection that the visual evoked response is maximal in a region well in front of the area centralis representation, and outside the stria'e area. Responses from visual I are of relatively low amplitude.

Cells whose receptive fields can be divided into excitatory and inhibitory regions are in their behaviour probably the simplest in the cat's striate cortex. We therefore assume that these cells receive their projections directly from the lateral geniculate body. It is not difficult to think of a model for this: Fig. 2 shows a possible scheme for the

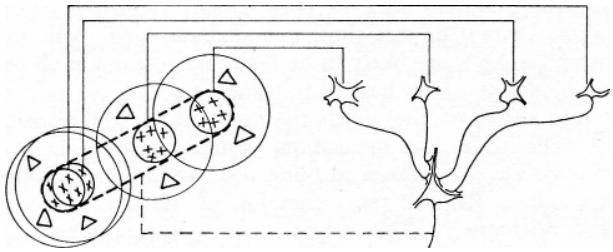

Fig. 2. Possible scheme for explaining the organization of simple receptive fields. A large number of lateral geniculate cells, of which four are illustrated in the upper right in the figure, have receptive fields with 'on'-centres arranged along a straight line on the retina. All of these project upon a single cortical cell, and the synapses are supposed to be excitatory. The receptive field of the cortical cell will then have an elongated 'on'-centre indicated by the interrupted lines in the receptive-field diagram to the left of the figure. (From Hubel and Wiesel 1962, text-fig. 19.)

elaboration of one type of simple receptive field. One can imagine that the cortical cell receives projections from a large number of geniculate cells, of which only four are illustrated, and that the fields of the geniculate cells have extensively overlapping 'on'-centres arranged along a straight line so as to cover a long narrow area. Illuminating any of these geniculate field-centres evokes strong discharges from some geniculate cells, and these impulses fire the cortical cell. The afferent geniculate cells whose field peripheries are illuminated will of course have their firing suppressed at the same time, but we must assume that the excitatory effect overrides this. Such a model may not be correct in detail, but it seems to be the simplest one consistent with the experimental facts.

In the striate cortex we find cells of a second type, whose properties we have called 'complex'. These cells do not respond well to small spots of light, and it is not generally possible to map their fields into separate excitatory and inhibitory regions. When one does obtain such maps they do not help in explaining responses to. more complex patterns.

Complex cells respond well to just those stimuli that best activate simple cells, namely slits, dark bars, and edges. Just as with simple cells, the stimulus must be oriented in a direction that is specific for each cell. As before, we speak of this as the receptive-field axis orientation. A complex cell, however, differs from simple cells in that a stimulus is effective wherever it is placed in the receptive field, provided the orientation is appropriate. An example of the behaviour of a typical complex cell is shown in Fig. 3: this cell responded well to a dark bar, and it demanded only that the

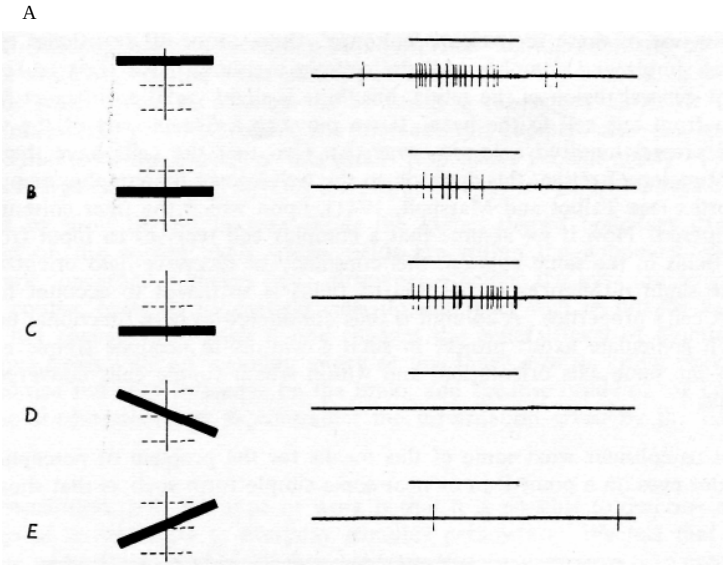

Fig. 3. Cell activated only by left (contralateral) eye over a field approximately 5x5°, situated 10° above and to the left of the area centralis. The cell responded best to a black horizontal rectangle, *Vs* X 6°, placed anywhere in the receptive field (A-C). Tilting the stimulus rendered it ineffective (D-E). The black bar was introduced against a light background during periods of 1 sec, indicated by the upper line in each record. Luminance of white background, 1.0 Iog_{10} cd/m^2; luminance of black part, 0.0 Iog_{10} cd/m^2. A lesion, made while recording from the cell, was found in layer 2 of apical segment of post-lateral gyrus. (From Hubel and Wiesel, 1962, text-fig. 7.)

bar be oriented horizontally somewhere within a fairly extensive receptive field. Placing the image anywhere within this area caused the cell to fire; covering the same area with the image placed at an oblique angle or vertically had no effect at all.

It is very difficult to account for this type of behaviour by supposing that complex cells are connected directly with lateral geniculate cells. A complex cell behaves as though it received its afferents from a large number of cortical cells with simple fields, all of these fields having the same axis orientation, but varying slightly from one to the next in their retinal positions. By this scheme, the cell of Fig. 3 would receive projections from a large number of cells of type D, in Fig. 1, all the corresponding simple fields having horizontal orientations but with staggered retinal positions, some higher, others lower. Presumably wherever within the complex field the horizontal stimulus fell it would stimulate simple fields projecting to the complex cell, and so cause the complex cell to fire. An oblique stimulus would activate none of the simple cells, and consequently would not activate the complex one. This cell thus acts as though it had the function of responding to the abstract quality 'horizontal', irrespsctive of exact retinal position.

The idea that a complex cell receives its input from a large number of simple cells all having the same receptive-field orientation has a remarkable parallel in the functional anatomy of the cat's striate cortex. Cells that are close neighbors almost always have receptive-field axis orientations that are, as far as one can tell, identical. By making long penetrations through the cortex one can show that the regions of constant orientation extend from surface to white matter, with walls perpendicular to the cortical layers (Hubel and Wiesel, 1962, Part III; 1963).

Within one of these regions, or 'columns', there occur all functional types of cells, including simple and complex. All the cells in a column have their receptive fields in the same general region of the retina, but there is slight variation in *exact* receptive-field position from one cell to the next. If we move to a distant part of the visual cortex, perhaps several hundred columns away, we find that the cells have their fields in a different region of retina; this depends on the well-known topographic mapping of retina onto cortex (see Talbot and Marshall, 1941), upon which the finer columnar system is superimposed. Now if we assume that a complex cell receives its input from cells with simple fields in the same column, this constancy of receptive-rield orientation together with the slight differences in position of fields is sufficient to account for all of the complex cell's properties. A column is thus considered to be a functional unit of cortex, to which geniculate axons project in such a way as to produce simple cortical fields all with the same axis orientation, and within which simple cells converge upon complex cells.

Now let us consider what some of this means for the problem of perception. Suppose we fix our eyes on a point P in or near some simple form such as that shown in Fig. 4,

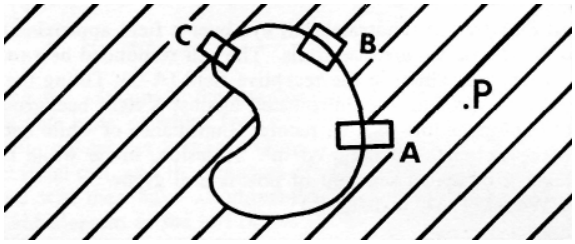

Fig. 4

consisting of a homogeneous white shape against a darker background. We can ask how cells in the visual cortex will be influenced by the retinal image that this form produces. Any small region of the figure, such as that shown in rectangle A, will influence a certain set of simple cells in the hemisphere. These cells, since they are influenced by region A, must have a stimulus preference for edges (i.e., be of the type G, Fig. 1), and they must have their fields in a certain particular part of the retina, such that the boundary between excitatory and inhibitory areas coincides with the boundary between light and darkness in the retinal image of A. Another small region B will activate another set of cells of type G, and their fields must have a different retinal position and orientation. The form as a whole will activate the larger population made up of many such groups (corresponding to squares B, C, etc.). If we move our eye or if we displace the form but keep the eye fixed, the population of simple cells influenced by the stimulus will change completely.

Instead of simple cells, let us now consider the set of complex cells that is activated by the form. Just as before, there will be a large set of complex cells activated by the form as a whole, some for each small region A, B, C, etc. If we move the eye or the stimulus, any given complex cell will cease to be influenced only if the displacement is large enough to take the boundary completely outside of the cell's receptive field. A displacement of the whole form, provided it is not too great, will therefore not greatly change the population of complex cells that is influenced by the boundaries

of the form. The population of complex cells influenced by the form will thus depend more on the shape than on the exact position of the image on the retina. The stimulus may even be made larger or smaller—as by bringing the object closer or removing it—without necessarily greatly changing the population of complex cells that is affected. It is possible that some mechanism of this sort is responsible for our ability to recognize an object to a large extent irrespective of the position of the image on the retina.

Note that by itself the bright area *inside* the kidney-shaped boundary exerts little if any effect on the cortical cells whose fields are within the boundary. As far as these cells are concerned it makes little difference whether the eyes are open or not. This is, of course, because the cortical cells do not react well to diffuse light; their firing does not change very much if one changes the general level of illumination of their receptive fields. We are possibly aware of this inner area as bright only because of its boundaries and *their* influence on the brain, and because inside of the boundaries there are no further contrasts to contradict the information given by the boundaries themselves.

A general conclusion from this type of work is that it is possible to describe a cortical cell in terms of its responses to everyday stimulus parameters. We feel that we have at least some understanding of a cell if we can say that its duty is to take care of a 1 ° by 1° region of retina, 6° to the left of the fovea and 4° above it, and to fire whenever a light line on a dark background appears, provided it is inclined at about 45°. Yet while such a description of a cell's responses to natural stimuli is valuable, it alone may tell us very little about the function of the cell, or of the larger structure of which the cell is a part. What we especially wish to know is how the incoming information has been transformed. Our understanding of a complex cell is greatly aided by knowing about simple cells, and our understanding of simple cells by knowing about 'on'- and 'off-centre geniculate cells. The schemes proposed to explain the properties of simple and complex cells are simply an interpretation of these comparisons. Of course, the comparisons have a reciprocal value: we have a greater appreciation of the properties of geniculate cells if we know that by a process of convergence simple cortical fields will result. No doubt we will have a better idea of the role complex cells play in vision when we examine the fields of the cells to which *they* project. How far the process can be carried is anybody's guess.

One further comment may be made concerning wiring diagrams of the kind suggested to account for simple and complex cortical fields. At present there is no direct proof for proposals of this sort. Instead we have to be satisfied with indirect evidence such as that provided by the columnar architecture. For direct evidence one would need to record from a cortical cell, and then in turn record from each of the hundreds of fibres ending on that cell; one would also need to know whether each synapse was excitatory or inhibitory (and if inhibitory, I suppose, whether it was presynaptic or postsynaptic). The techniques for doing anything like this are far out of our reach, and probably will continue to be for some time. Nevertheless it is satisfying to be able to propose simple schemes that *could* explain the properties of the cells we study. None of the transformations, from retina to geniculate, from geniculate to simple cortical cells, or from simple cells to complex cells, need involve anything more complicated than common, well-known physiological processes such as impulses, convergence, synaptic excitation, and synaptic inhibition. This may turn out to be so for other areas in the central nervous system. If it does, then the use of single-cell recording techniques in conjunction with natural stimuli may produce a startling increase in our knowledge of brain function in the next few years.

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