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Brain Mechanisms of Vision

A functional architecture that may underlie processing of sensory information in the cortex is revealed by studies of the activity and the organization in space of neurons in the primary visual cortex

by David H. Hubel and Torsten N. Wiesel

Viewed as a kind of invention by evolution, the cerebral cortex must be one of the great success stories in the history of living things. In vertebrates lower than mammals the cerebral cortex is minuscule, if it can be said to exist at all. Suddenly impressive in the lowest mammals, it begins to dominate the brain in carnivores, and it increases explosively in primates; in man it almost completely envelops the rest of the brain, tending to obscure the other parts. The degree to which an animal depends on an organ is an index of the organ's importance that is even more convincing than size, and dependence on the cortex has increased rapidly as mammals have evolved. A mouse without a cortex appears fairly normal, at least to casual inspection; a man without a cortex is almost a vegetable, speechless, sightless, senseless.

Understanding of this large and indispensable organ is still woefully deficient. This is partly because it is very complex, not only structurally but also in its functions, and partly because neurobiologists' intuitions about the functions have so often been wrong. The outlook is changing, however, as techniques improve and as investigators learn how to deal with the huge numbers of intricately connected neurons that are the basic elements of the cortex, with the impulses they carry and with the synapses that connect them. In this article we hope to sketch the present state of knowledge of one subdivision of the cortex: the primary visual cortex (also known as the striate cortex or area 17), the most elementary of the cortical regions concerned with vision. That will necessarily lead us into the related subject of visual perception, since the workings of an organ cannot easily be separated from its biological purpose.

The cerebral cortex, a highly folded plate of neural tissue about two millimeters thick, is an outermost crust wrapped over the top of, and to some extent tucked under, the cerebral hemispheres. In man its total area, if it were spread out, would be about 1.5 square

feet. (In a 1963 article in *Scientific American* one of us gave the area as 20 square feet and was quickly corrected by a neuroanatomist friend in Toronto, who said he thought it was 1.5 square feet—"at least that is what Canadians have.") The folding is presumably mainly the result of such an unlikely structure's having to be packed into a box the size of the skull.

A casual glance at cortical tissue under a microscope shows vast numbers of neurons: about 10^5 (100,000) for each square millimeter of surface, suggesting that the cortex as a whole has some 10^{10} (10 billion) neurons. The cell bodies are arranged in half a dozen layers that are alternately cell-sparse and cell-rich. In contrast to these marked changes in cell density in successive layers at different depths in the cortex there is marked uniformity from place to place in the plane of any given layer and in any direction within that plane. The cortex is morphologically rather uniform in two of its dimensions.

One of the first great insights about cortical organization came late in the 19th century, when it was gradually realized that this rather uniform plate of tissue is subdivided into a number of different regions that have very different functions. The evidence came from clinical, physiological and anatomical sources. It was noted that a brain injury, depending on its location, could cause paralysis or blindness or numbness or speech loss; the blindness could be total or limited to half or less of the visual world, and the numbness could involve one limb or a few fingers. The consistency of the relation between a given defect and the location of the lesion gradually led to a charting of the most obvious of these specialized regions, the visual, auditory, somatic sensory (body sensation), speech and motor regions.

In many cases a close look with a microscope at cortex stained for cell bodies showed that in spite of the relative uniformity there were structural variations, particularly in the layering pattern, that correlated well with the clinically defined subdivisions. Additional confirmation came from observations

of the location (at the surface of the brain) of the electrical brain waves produced when an animal was stimulated by touching the body, sounding clicks or tones in the ear or flashing light in the eye. Similarly, motor areas could be mapped by stimulating the cortex electrically and noting what part of the animal's body moved.

This systematic mapping of the cortex soon led to a fundamental realization: most of the sensory and motor areas contained systematic two-dimensional maps of the world they represented. Destroying a particular small region of cortex could lead to paralysis of one arm; a similar lesion in another small region led to numbness of one hand or of the upper lip, or blindness in one small part of the visual world; if electrodes were placed on an animal's cortex, touching one limb produced a correspondingly localized series of electric potentials. Clearly the body was systematically mapped onto the somatic sensory and motor areas; the visual world was mapped onto the primary visual cortex, an area on the occipital lobe that in man and in the macaque monkey (the animal in which our investigations have mainly been conducted) covers about 15 square centimeters.

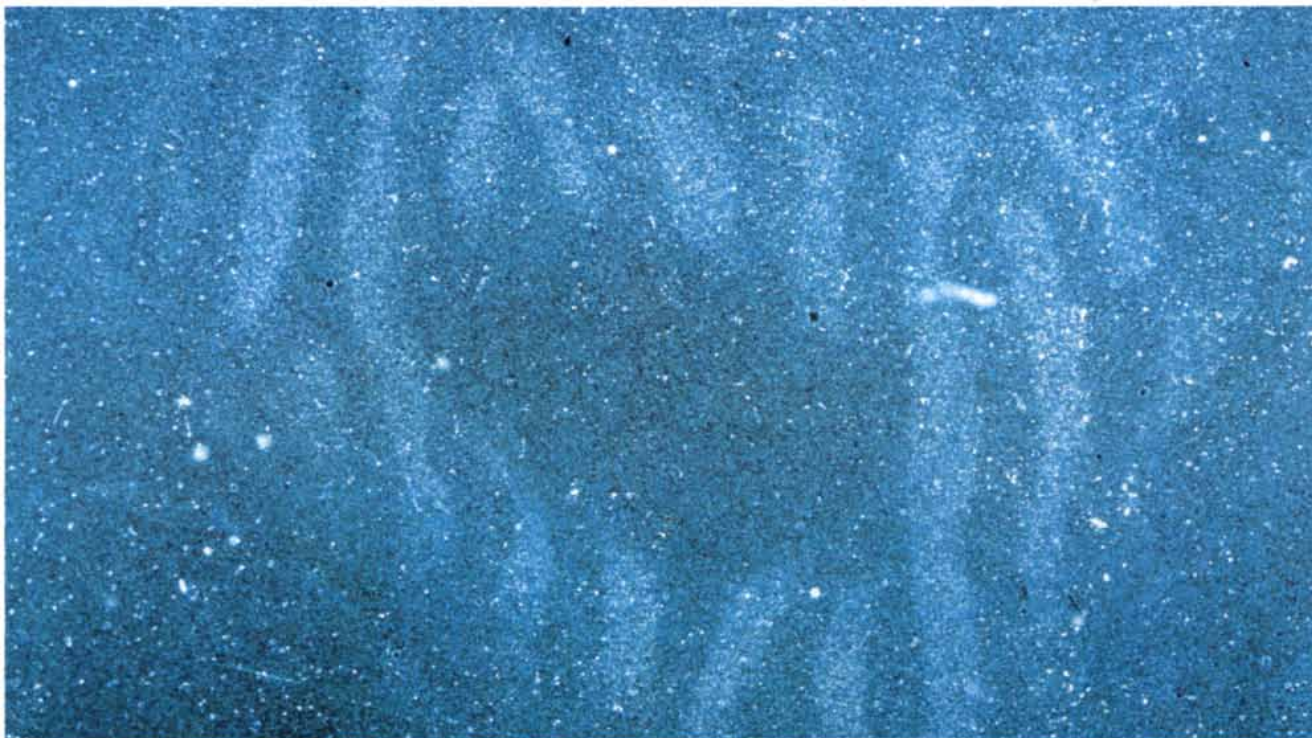
In the primary visual cortex the map is uncomplicated by breaks and discontinuities except for the remarkable split of the visual world down the exact middle, with the left half projected to the right cerebral cortex and the right half projected to the left cortex. The map of the body is more complicated and is still perhaps not completely understood. It is nonetheless systematic, and it is similarly crossed, with the right side of the body projecting to the left hemisphere and the left side projecting to the right hemisphere. (It is worth remarking that no one has the remotest idea why there should be this amazing tendency for nervous-system pathways to cross.)

An important feature of cortical maps is their distortion. The scale of the maps varies as it does in a Mercator projection, the rule for the cortex being that



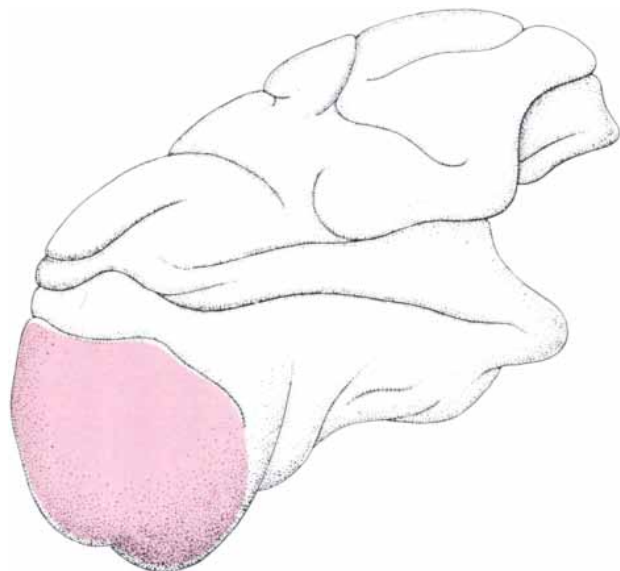
OCULAR-DOMINANCE COLUMNS, one of the two major systems that characterize the functional architecture of the primary visual cortex, are revealed as periodic bright patches in this dark-field autoradiograph of a section of macaque monkey cortex. The columns (actually curving slabs of cortex, seen here in cross section in a brain slice cut perpendicularly to the surface) are regions in which all neurons respond more actively to the right eye than to the left one; dark regions separating the bright patches are columns of left-eye prefer-

ence. The autoradiograph was made by injecting a radioactively labeled amino acid into the right eye of an anesthetized animal. The amino acid was taken up by cell bodies in the retina and transported via the lateral geniculate nucleus, a way station in the brain, to cells in the cortex. A brain slice was coated with a photographic emulsion, which was exposed for several months and then developed. Exposed silver grains overlying the regions of radioactivity form the light-scattering patches that represent ocular-dominance columns.

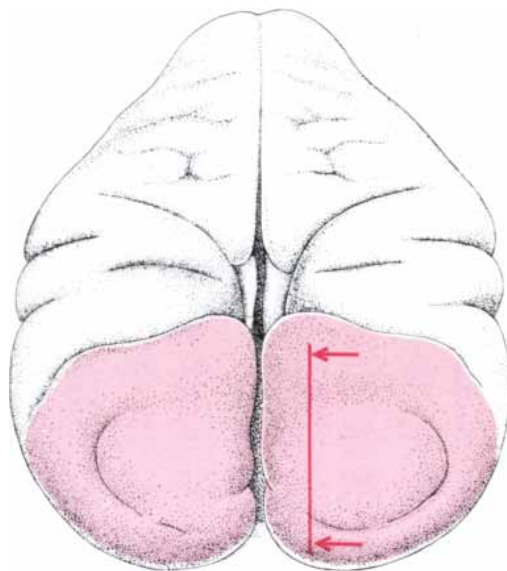


DOMINANCE PATTERN is seen face on in an axonal-transport autoradiograph of a brain section parallel, rather than perpendicular, to the surface of the primary visual cortex. As can be seen in the autoradiograph at the top of the page, the label is brightest in one layer of the folded cortex, layer IV. This is the level at which the axons bringing visual information to the cortex terminate and where

the label therefore accumulates. This section was cut in a plane tangential to the dome-shaped surface of the cortex and just below layer IV, which therefore appears as a ring of roughly parallel bright bands. These are the radioactively labeled ocular-dominance regions, which are now seen from above instead of edge on. The actual width of the ocular-dominance regions is typically about .4 millimeter.



PRIMARY VISUAL CORTEX, also known as the striate cortex or area 17, is a region of the cerebral cortex: a layered plate of neurons that envelops the primate brain. In the macaque brain, seen here from the side (*left*) and from above and behind (*right*), the primary visual cortex (*colored areas*) occupies most of the exposed surface of



the two occipital lobes. It also curves around the medial surface between the two cerebral hemispheres. It continues in a complex fold underneath the convex outer surface, as is shown in a parasagittal section (*see top illustration on opposite page*) that was cut along the colored line and is viewed in the direction indicated by the arrows.

the regions of highest discrimination or delicacy of function occupy relatively more cortical area. For the body surface, a millimeter of surface on the fingers, the lips or the tongue projects to more cortex than a millimeter of trunk, buttocks or back; in vision the central part of the retina has a representation some 35 times more detailed than the far peripheral part.

Important as the advances in mapping cortical projections were, they tended for some time to divert thought from the real problem of just how the brain analyzes information. It was as though the representation could be an end in itself instead of serving a more subtle purpose—as though what the cortex did was to cater to some little green man who sat inside the head and surveyed images playing across the cortex. In the course of this article we shall show that, for vision at least, the world is represented in a far more distorted way; any little green man trying to glean information from the cortical projection would be puzzled indeed.

The first major insight into cortical organization was nonetheless the recognition of this subdivision into areas having widely different functions, with a tendency to ordered mapping. Just how many such areas there are has been a subject of wide speculation. Anatomists' estimates have on the whole been rather high—up to several hundred areas, depending on the individual worker's sensitivity to fine differences in microscopic patterns and sometimes also on his ability to fool himself. Physiologists began with lower estimates, but lately, with more powerful mapping methods, they

have been revising their estimates upward. The important basic notion is that information on any given modality such as sight or sound is transmitted first to a primary cortical area and from there, either directly or via the thalamus, to successions of higher areas. A modern guess as to the number of cortical areas might be between 50 and 100.

The second major insight into cortical organization came from the work of the anatomist Santiago Ramón y Cajal and his pupil Rafael Lorente de Nó. This was the realization that the operations the cortex performs on the information it receives are local. What that means can best be understood by considering the wiring diagram that emerged from the Golgi method used by Cajal and Lorente de Nó. In essence the wiring is simple. Sets of fibers bring information to the cortex; by the time several synapses have been traversed the influence of the input has spread vertically to all cell layers; finally several other sets of fibers carry modified messages out of the area. The detailed connections between inputs and outputs differ from one area to the next, but within a given area they seem to be rather stereotyped. What is common to all regions is the local nature of the wiring. The information carried into the cortex by a single fiber can in principle make itself felt through the entire thickness in about three or four synapses, whereas the lateral spread, produced by branching trees of axons and dendrites, is limited for all practical purposes to a few millimeters, a small proportion of the vast extent of the cortex.

The implications of this are far-reaching. Whatever any given region of the cortex does, it does locally. At stages where there is any kind of detailed, systematic topographical mapping the analysis must be piecemeal. For example, in the somatic sensory cortex the messages concerning one finger can be combined and compared with an input from elsewhere on that same finger or with input from a neighboring finger, but they can hardly be combined with the influence from the trunk or from a foot. The same applies to the visual world. Given the detailed order of the input to the primary visual cortex, there is no likelihood that the region will do anything to correlate information coming in from both far above and far below the horizon, or from both the left and the right part of the visual scene. It follows that this cannot by any stretch of the imagination be the place where actual perception is enshrined. Whatever these cortical areas are doing, it must be some kind of local analysis of the sensory world. One can only assume that as the information on vision or touch or sound is relayed from one cortical area to the next the map becomes progressively more blurred and the information carried more abstract.

Even though the Golgi-method studies of the early 1900's made it clear that the cortex must perform local analyses, it was half a century before physiologists had the least inkling of just what the analysis was in any area of the cortex. The first understanding came in the primary visual area, which is now the best-understood of any cortical region and is still the only one where the analy-

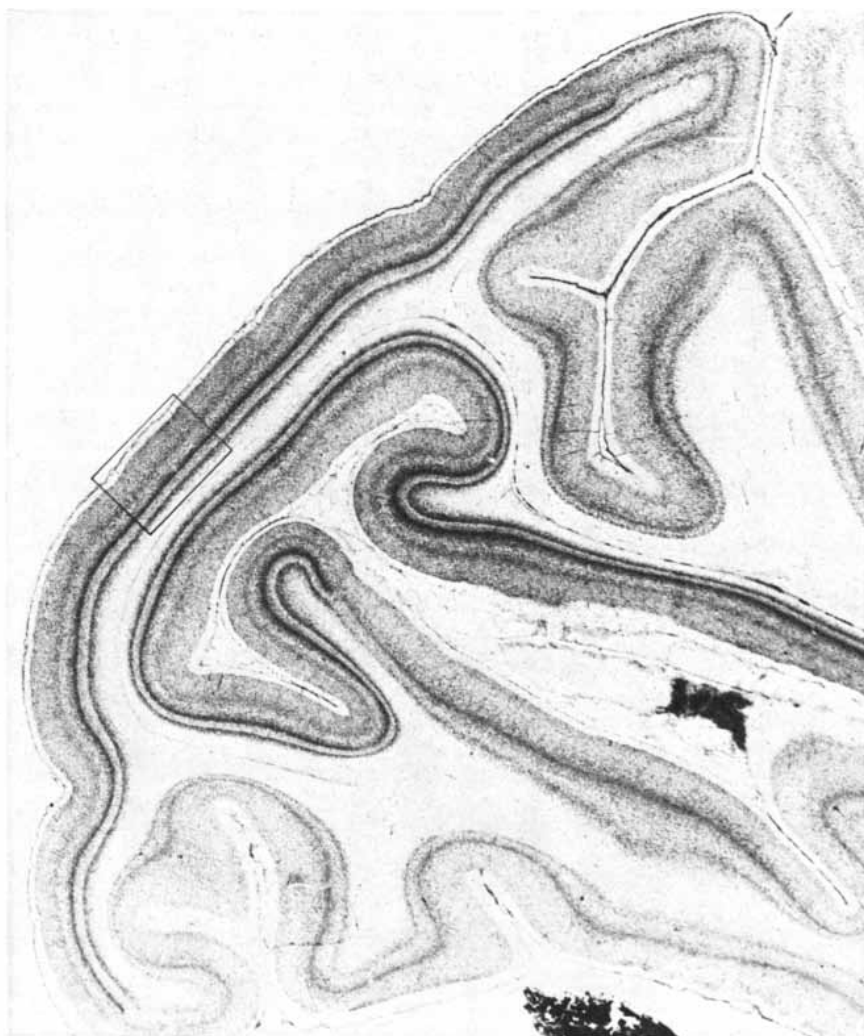
sis and consequent transformations of information are known in any detail. After describing the main transformations that take place in the primary visual cortex we shall go on to show how increasing understanding of these cortical functions has revealed an entire world of architectural order that is otherwise inaccessible to observation.

We can best begin by tracing the visual path in a primate from the retina to the cortex. The output from each eye is conveyed to the brain by about a million nerve fibers bundled together in the optic nerve. These fibers are the axons of the ganglion cells of the retina. The messages from the light-sensitive elements, the rods and cones, have already traversed from two to four synapses and have involved four other types of retinal cells before they arrive at the ganglion cells, and a certain amount of sophisticated analysis of the information has already taken place.

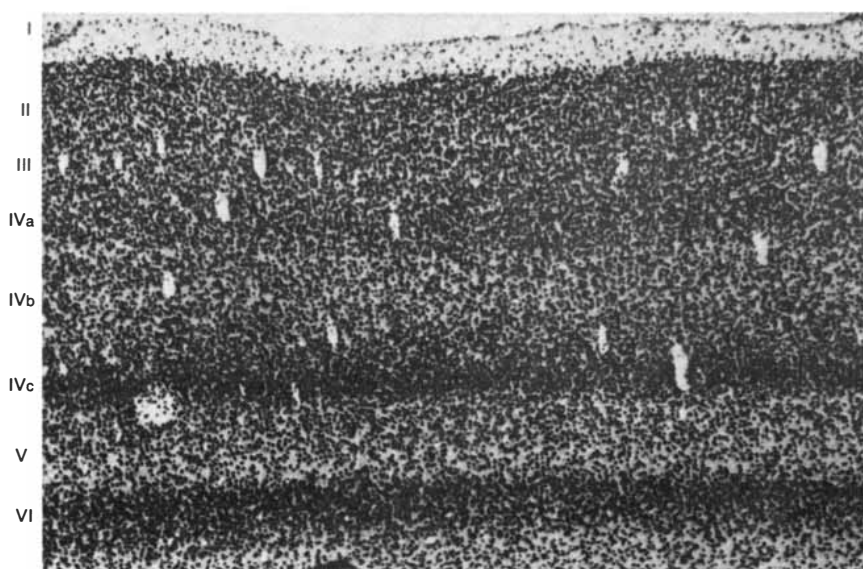
A large fraction of the optic-nerve fibers pass uninterrupted to two nests of cells deep in the brain called the lateral geniculate nuclei, where they make synapses. The lateral geniculate cells in turn send their axons directly to the primary visual cortex. From there, after several synapses, the messages are sent to a number of further destinations: neighboring cortical areas and also several targets deep in the brain. One contingent even projects back to the lateral geniculate bodies; the function of this feedback path is not known. The main point for the moment is that the primary visual cortex is in no sense the end of the visual path. It is just one stage, probably an early one in terms of the degree of abstraction of the information it handles.

As a result of the partial crossing of the optic nerves in the optic chiasm, the geniculate and the cortex on the left side are connected to the two left half retinas and are therefore concerned with the right half of the visual scene, and the converse is the case for the right geniculate and the right cortex. Each geniculate and each cortex receives input from both eyes, and each is concerned with the opposite half of the visual world.

To examine the workings of this visual pathway our strategy since the late 1950's has been (in principle) simple. Beginning, say, with the fibers of the optic nerve, we record with microelectrodes from a single nerve fiber and try to find out how we can most effectively influence the firing by stimulating the retina with light. For this one can use patterns of light of every conceivable size, shape and color, bright on a dark background or the reverse, and stationary or moving. It may take a long time, but sooner or later we satisfy ourselves that we have found the best stimulus for the cell being tested, in this case a ganglion cell of the retina. (Sometimes we are



SECTION OF VISUAL CORTEX along the colored line in the illustration on the opposite page was stained by the Nissl method, which makes cell bodies but not fibers visible. The visual cortex is seen to be a continuous layered sheet of neurons about two millimeters thick. The black rectangle outlines a section like the one that is further enlarged in the illustration below.



CROSS SECTION OF PRIMARY VISUAL CORTEX in the macaque, stained here by the Nissl method and enlarged about 35 diameters, shows the layered structure and gives the conventional designations of the six layers (*left*). The white gaps are sectioned blood vessels.

wrong!) We note the results and then go on to another fiber. After studying a few hundred cells we may find that new types become rare. Satisfied that we know roughly how the neurons at this stage work, we proceed to the next stage (in this case the geniculate) and repeat the process. Comparison of the two sets of results can tell us something about what the geniculate does. We then go on to the next stage, the primary cortex, and repeat the procedure.

Working in this way, one finds that both a retinal ganglion cell and a geniculate cell respond best to a roughly circular spot of light of a particular size in a particular part of the visual field. The size is critical because each cell's receptive field (the patch of retinal receptor cells supplying the cell) is divided, with an excitatory center and an inhibitory surround (an "on center" cell) or exactly the reverse configuration (an "off center" cell). This is the center-surround configuration first described by Stephen W. Kuffler at the Johns Hopkins University School of Medicine in 1953. A spot exactly filling the center of an on-center cell is therefore a more effective stimulus than a larger spot that invades the inhibitory area, or than diffuse light. A line stimulus (a bar of light) is effective if it covers a large part of the center region and only a small part of the surround. Because these cells have circular

symmetry they respond well to such a line stimulus whatever its orientation. To sum up, the retinal ganglion cells and the cells of the lateral geniculate—the cells supplying the input to the visual cortex—are cells with concentric, center-surround receptive fields. They are primarily concerned not with assessing levels of illumination but rather with making a comparison between the light level in one small area of the visual scene and the average illumination of the immediate surround.

The first of the two major transformations accomplished by the visual cortex is the rearrangement of incoming information so that most of its cells respond not to spots of light but to specifically oriented line segments. There is a wide variety of cell types in the cortex, some simpler and some more complex in their response properties, and one soon gains an impression of a kind of hierarchy, with simpler cells feeding more complex ones. In the monkey there is first of all a large group of cells that behave (as far as is known) just like geniculate cells: they have circularly symmetrical fields. These cells are all in the lower part of one layer, called layer IV, which is precisely the layer that receives the lion's share of the geniculate input. It makes sense that these least sophisticated cortical cells should be

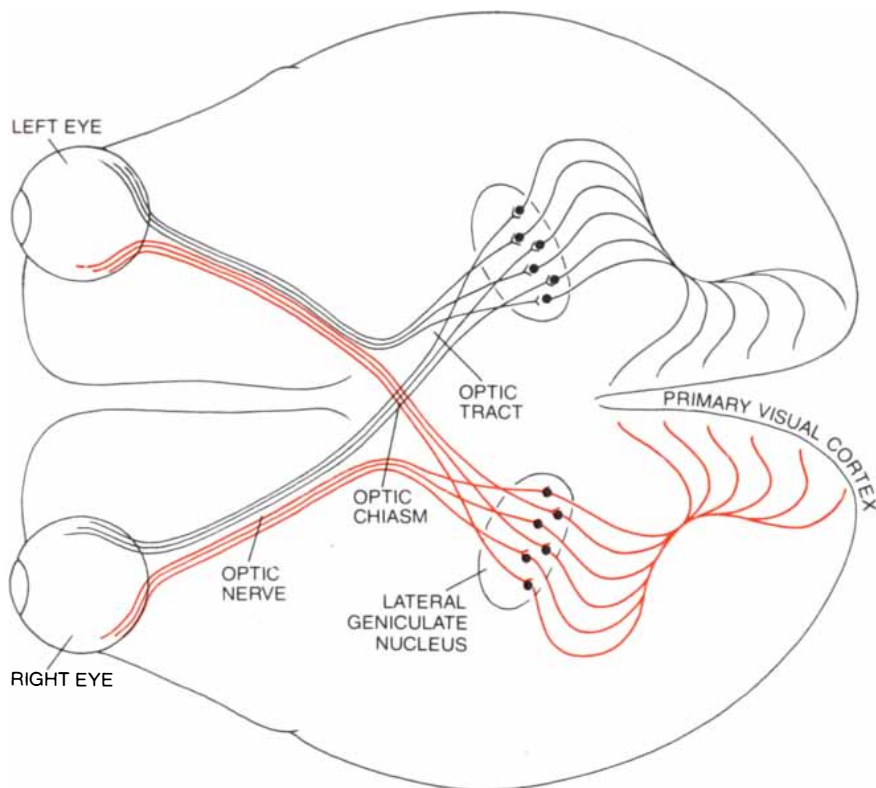
the ones most immediately connected to the input.

Cells outside layer IV all respond best to specifically oriented line segments. A typical cell responds only when light falls in a particular part of the visual world, but illuminating that area diffusely has little effect or none, and small spots of light are not much better. The best response is obtained when a line that has just the right tilt is flashed in the region or, in some cells, is swept across the region. The most effective orientation varies from cell to cell and is usually defined sharply enough so that a change of 10 or 20 degrees clockwise or counterclockwise reduces the response markedly or abolishes it. (It is hard to convey the precision of this discrimination. If 10 to 20 degrees sounds like a wide range, one should remember that the angle between 12 o'clock and one o'clock is 30 degrees.) A line at 90 degrees to the best orientation almost never evokes any response.

Depending on the particular cell, the stimulus may be a bright line on a dark background or the reverse, or it may be a boundary between light and dark regions. If it is a line, the thickness is likely to be important; increasing it beyond some optimal width reduces the response, just as increasing the diameter of a spot does in the case of ganglion and geniculate cells. Indeed, for a particular part of the visual field the geniculate receptive-field centers and the optimal cortical line widths are comparable.

Neurons with orientation specificity vary in their complexity. The simplest, which we call "simple" cells, behave as though they received their input directly from several cells with center-surround, circularly symmetrical fields—the type of cells found in layer IV. The response properties of these simple cells, which respond to an optimally oriented line in a narrowly defined location, can most easily be accounted for by requiring that the centers of the incoming center-surround fields all be excitatory or all be inhibitory, and that they lie along a straight line. At present we have no direct evidence for this scheme, but it is attractive because of its simplicity and because certain kinds of indirect evidence support it. According to the work of Jennifer S. Lund of the University of Washington School of Medicine, who in the past few years has done more than anyone else to advance the Golgi-stain anatomy of this cortical area, the cells in layer IV project to the layers just above, which is roughly where the simple cells are found.

The second major group of orientation-specific neurons are the far more numerous "complex" cells. They come in a number of subcategories, but their main feature is that they are less particular about the exact position of a line.

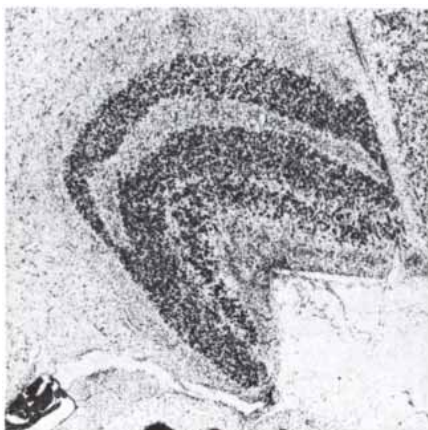


VISUAL PATHWAY is traced schematically in the human brain, seen here from below. The output from the retina is conveyed, by ganglion-cell axons bundled in the optic nerves, to the lateral geniculate nuclei; about half of the axons cross over to the opposite side of the brain, so that a representation of each half of the visual scene is projected on the geniculate of the opposite hemisphere. Neurons in the geniculates send their axons to the primary visual cortex.

RIGHT EYE



LEFT EYE



RIGHT EYE



LATERAL GENICULATE NUCLEUS of a normal monkey (*left*) is a layered structure in which cells in layers 1, 4 and 6 (numbered from bottom to top) receive their input from the eye on the opposite side and those in layers 2, 3 and 5 receive information from the eye on the same side. The maps are in register, so that the neurons along

any radius (*black line*) receive signals from the same part of the visual scene. The layered nature of the input is demonstrated in the two geniculata of an animal that had vision in the left eye only (*two micrographs at right*): in each geniculate cells in the three layers with input from right eye have atrophied. Geniculata are enlarged 10 diameters.

Complex cells behave as though they received their input from a number of simple cells, all with the same receptive-field orientation but differing slightly in the exact location of their fields. This scheme readily explains the strong steady firing evoked in a complex cell as a line is kept in the optimal orientation and is swept across the receptive field. With the line optimally oriented many cells prefer one direction of movement to the opposite direction. Several possible circuits have been proposed to explain this behavior, but the exact mechanism is still not known.

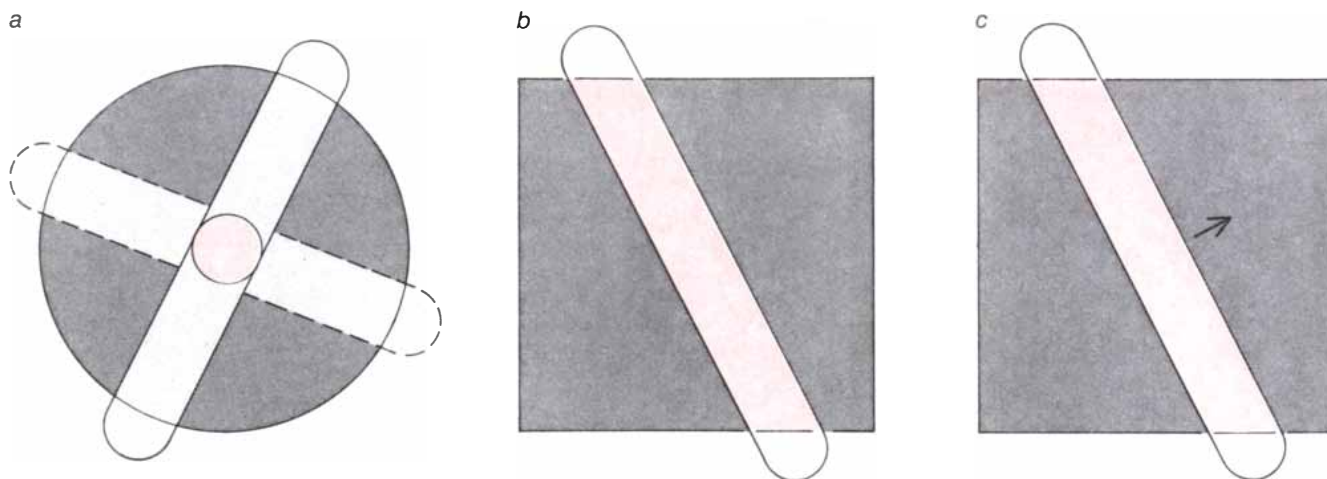
Although there is no direct evidence that orientation-sensitive cells have anything to do with visual perception, it is certainly tempting to think they represent some early stage in the brain's anal-

ysis of visual forms. It is worth asking which cells at this early stage would be expected to be turned on by some very simple visual form, say a dark blob on a light background. Any cell whose receptive field is entirely inside or outside the boundaries of such an image will be completely unaffected by the figure's presence because cortical cells effectively ignore diffuse changes in the illumination of their entire receptive fields.

The only cells to be affected will be those whose field is cut by the borders. For the circularly symmetrical cells the ones most strongly influenced will be those whose center is grazed by a boundary (because for them the excitatory and inhibitory subdivisions are most unequally illuminated). For the orientation-specific cells the only ones to be ac-

tivated will be those whose optimal orientation happens to coincide with the prevailing direction of the border. And among these the simple cells will be much more exacting than the complex ones, responding optimally only when the border falls along a line separating an excitatory and an inhibitory region. It is important to realize that this part of the cortex is operating only locally, on bits of the form; how the entire form is analyzed or handled by the brain—how this information is worked on and synthesized at later stages, if indeed it is—still not known.

The second major function of the monkey visual cortex is to combine the inputs from the two eyes. In the lateral geniculate nuclei a neuron may re-



RECEPTIVE FIELDS of various cells in the visual pathway are compared. Retinal ganglion cells and neurons in the lateral geniculate nucleus have circular fields with either an excitatory center and an inhibitory surround (*a*) or the opposite arrangement. A spot of light falling on the center stimulates a response from such a cell; so does a bar of light falling on the field in any orientation, provided it falls on the center. In the visual cortex there is a hierarchy of neurons with in-

creasingly complex response properties. The cortical cells that receive signals directly from the geniculate have circularly symmetrical fields. Cortical cells farther along the pathway, however, respond only to a line stimulus in a particular orientation. A "simple" cell (*b*) responds to such a line stimulus only in a particular part of its field. A "complex" cell (*c*) responds to a precisely oriented line regardless of where it is in its field and also to one moving in a particular direction (*arrow*).

spond to stimulation of the left eye or of the right one, but no cell responds to stimulation of both eyes. This may seem surprising, since each geniculate receives inputs from both eyes, but the fact is that the geniculata are constructed in a way that keeps inputs from the two eyes segregated. Each geniculate body is divided into six layers, three left-eye layers interdigitated with three right-eye ones. The opposite-side half of the visual world is mapped onto each layer (with the six maps in precise register, so that in a radial pathway traversing the six layers the receptive fields of all the cells encountered have virtually identical positions in the visual field). Since any one layer has input from only one eye, the individual cells of that layer must be monocular.

Even in the visual cortex the neurons to which the geniculate cells project directly, the circularly symmetrical cells in layer IV, are all (as far as we can tell) strictly monocular; so are all the simple cells. Only at the level of the complex cells do the paths from the two eyes converge, and even there the blending of information is incomplete and takes a special form. About half of the complex cells are monocular, in the sense that any one cell can be activated only by stimulating one eye. The rest of the cells can be influenced independently by both eyes.

If one maps the right-eye and left-eye receptive fields of a binocular cell (by stimulating first through one eye and then through the other) and compares the two fields, the fields turn out to have identical positions, levels of complexity, orientation and directional preference; everything one learns about the cell by stimulating one eye is confirmed through the other eye. There is only one exception: if first one eye and then the other are tested with identical stimuli, the two responses are usually not quantitatively identical; in many cases one eye is dominant, consistently producing a higher frequency of firing than the other eye.

From cell to cell all degrees of ocular dominance can be found, from complete monopoly by one eye through equality to exclusive control by the other eye. In the monkey the cells with a marked eye preference are somewhat commoner than the cells in which the two eyes make about equal contributions. Apparently a binocular cell in the primary visual cortex has connections to the two eyes that are qualitatively virtually identical, but the density of the two sets of connections is not necessarily the same.

It is remarkable enough that the elaborate sets of wiring that produce specificity of orientation and of direction of movement and other special properties

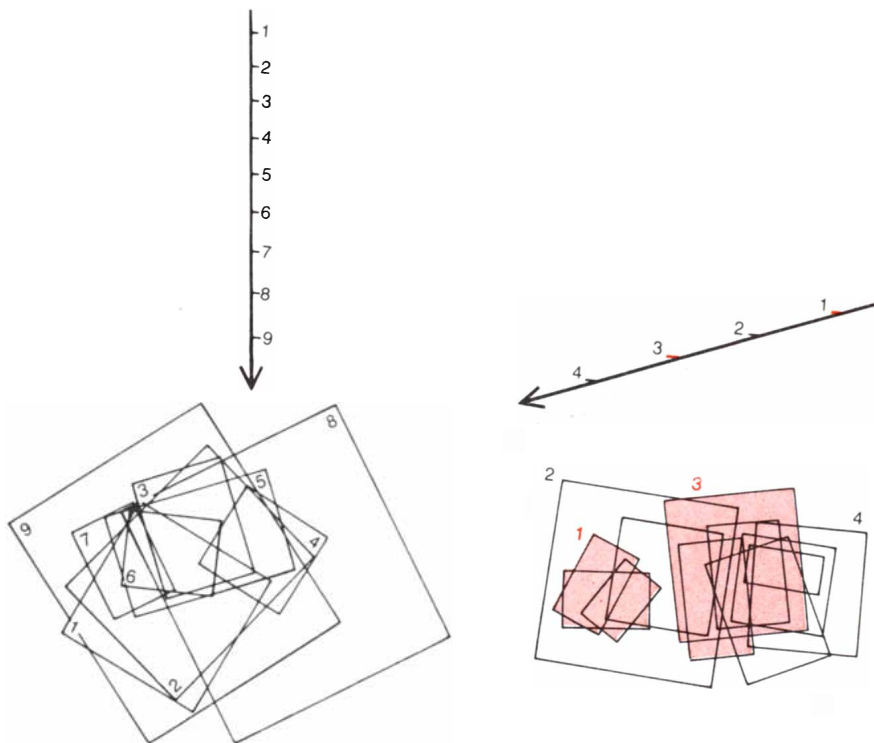
should be present in two duplicate copies. It is perhaps even more surprising that all of this can be observed in a newborn animal. The wiring is mostly innate, and it presumably is genetically determined. (In one particular respect, however, some maturation of binocular wiring does take place mostly after birth.)

We now turn to a consideration of the way these cells are grouped in the cortex. Are cells with similar characteristics—complexity, receptive-field position, orientation and ocular dominance—grouped together or scattered at random? From the description so far it will be obvious that cells of like complexity tend to be grouped in layers, with the circularly symmetrical cells low in layer IV, the simple cells just above them and the complex cells in layers II, III, V and VI. Complex cells can be further subcategorized, and the ones found in each layer are in a number of ways very different.

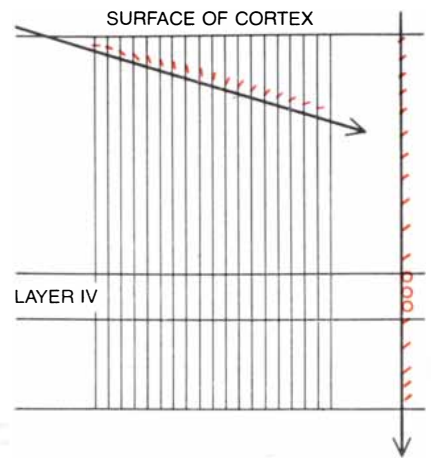
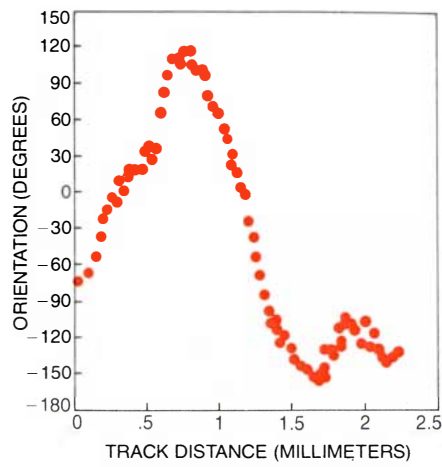
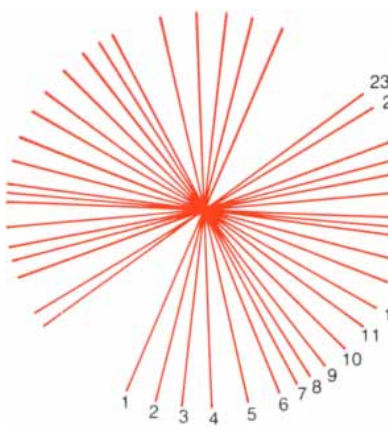
These differences from layer to layer take on added interest in view of the important discovery, confirmed by several physiologists and anatomists during the past few decades, that fibers projecting from particular layers of the cortex have particular destinations. For example, in the visual cortex the deepest layer, layer VI, projects mainly (perhaps only) back to the lateral geniculate body; layer V projects to the superior colliculus, a visual station in the mid-brain; layers II and III send their projections to other parts of the cortex. This relation between layer and projection site probably deserves to be ranked as a third major insight into cortical organization.

The next stimulus variable to be considered is the position of the receptive field in the visual field. In describing the lateral geniculate nucleus we pointed out that in each layer the opposite-half visual field forms an ordered topographical map. In the projection from lateral geniculate to primary visual cortex this order is preserved, producing a cortical map of the visual field. Given this ordered map it is no surprise that neighboring cells in this part of the cortex always have receptive fields that are close together; usually, in fact, they overlap. If one plunges a microelectrode into the cortex at a right angle to the surface and records from cell after cell (as many as 100 or 200 of them) in successively deeper layers, again the receptive fields mostly overlap, with each new field heaped on all the others. The extent of the entire pile of fields is usually several times the size of any one typical field.

There is some variation in the size of these receptive fields. Some of the variation is tied to the layering: the largest fields in any penetration tend to be in



POSITIONS OF RECEPTIVE FIELDS (numbered from 1 to 9) of cortical neurons mapped by an electrode penetrating at roughly a right angle to the surface are essentially the same (left), although the fields are different sizes and there is some scatter. In an oblique penetration (right) from two to four cells were recorded, at .1-millimeter intervals, at each of four sites (numbered from 1 to 4) one millimeter apart. Each group includes various sizes and some scatter, but now there is also a systematic drift: fields of each successive group of cells are somewhat displaced.



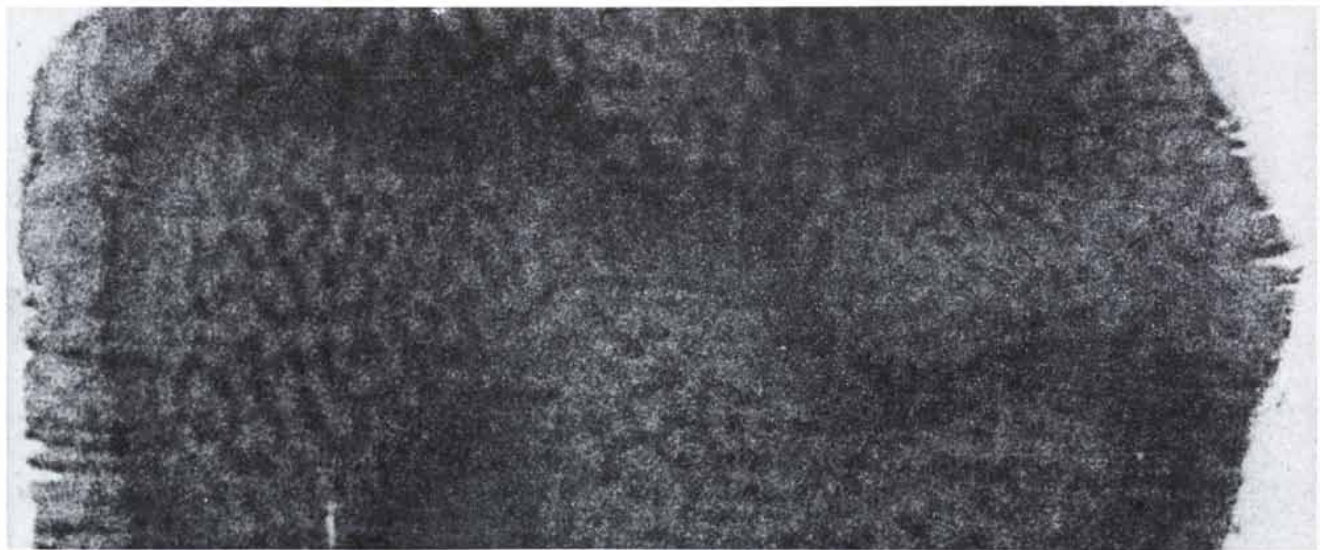
ORIENTATION PREFERENCES of 23 neurons encountered as a microelectrode penetrated the cortex obliquely are charted (*left*); the most effective tilt of the stimulus changed steadily in a counterclockwise direction. The results of a similar experiment are plotted (*center*); in this case, however, there were several reversals in direction of rotation. The results of a large number of such experiments, together

with the observation that a microelectrode penetrating the cortex perpendicularly encounters only cells that prefer the same orientation (apart from the circularly symmetrical cells in layer IV, which have no preferred orientation), suggested that the cortex is subdivided into roughly parallel slabs of tissue, with each slab, called an orientation column, containing neurons with like orientation specificity (*right*).



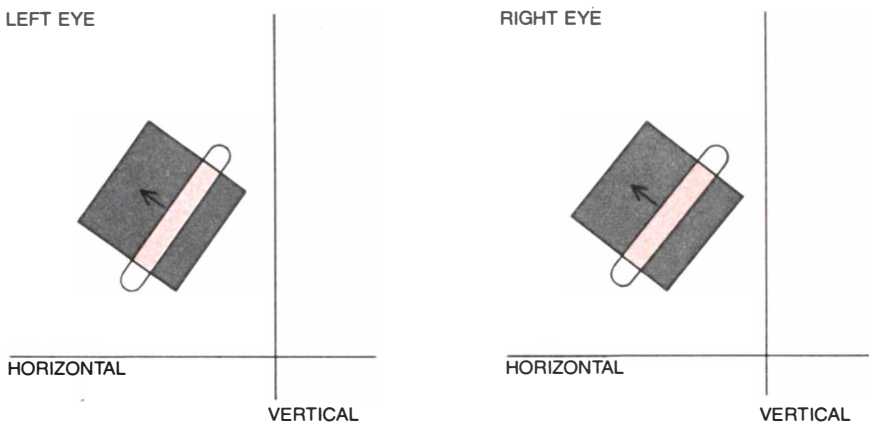
ORIENTATION COLUMNS are visualized as anatomical structures in a deoxyglucose autoradiograph made by the authors and Michael P. Stryker. Radioactively labeled deoxyglucose was injected into a monkey; it was taken up primarily by active neurons, and an early metabolite accumulated in the cells. Immediately after the in-

jection the animal was stimulated with a pattern of vertical stripes, so that cells responding to vertical lines were most active and became most radioactive. In this section perpendicular to surface active-cell regions are narrow bands about .5 millimeter apart. Layer IV (with no orientation preference) is, as expected, uniformly radioactive.



ORIENTATION PATTERN, seen face on, is unexpectedly complex. This deoxyglucose autoradiograph is of a section tangential to the somewhat curved layers of the cortex. The darker regions repre-

sent continuously labeled layer IV. In the other layers the orientation regions are intricately curved bands, something like the walls of a maze seen from above, but distance from one band to next is uniform.



BINOCULAR CELL in the cortex can be influenced independently by both eyes or more strongly by both eyes together. Here the left-eye and right-eye fields are mapped for a complex cell whose receptive field is in the upper left quadrant of the visual field. (The lines represent the horizontal and vertical meridians of the field, intersecting at the point of fixation.) The two receptive fields are identical, but the amount of response may differ depending on whether the left eye or the right eye is stimulated. Preference for one eye is called **ocular dominance**.

layers III, V and VI. The most important variation, however, is linked to eccentricity, or the distance of a cell's receptive field from the center of gaze. The size of the fields and the extent of the associated scatter in the part of the cortex that maps the center of gaze are tiny compared to the size and amount of scatter in the part that maps the far periphery. We call the pile of superimposed fields that are mapped in a penetration beginning at any point on the cortex the "aggregate field" of that point. The size of the aggregate field is obviously a function of eccentricity.

If the electrode penetrates in an oblique direction, almost parallel to the surface, the scatter in field position from cell to cell is again evident, but now there is superimposed on the scatter

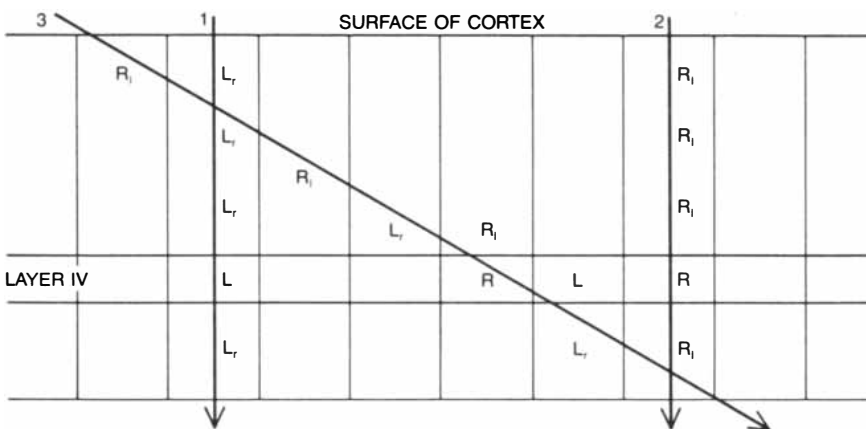
a consistent drift in field position, its direction dictated by the topographical map of the visual fields. And an interesting regularity is revealed: it turns out that moving the electrode about one or two millimeters always produces a displacement in visual field that is roughly enough to take one into an entirely new region. The movement in the visual field, in short, is about the same as the size of the aggregate receptive field. For the primary visual cortex this holds wherever the recording is made. At the center of gaze the fields and their associated scatter are tiny, but so is the displacement corresponding to a one-millimeter movement along the cortex. With increasing eccentricity (farther out in the visual field) both the field and scatter, in parallel fashion. It seems that every-

where a block of cortex about one or two millimeters in size is what is needed to take care of a region of the visual world equivalent to the size of an aggregate field.

These observations suggest the way the visual cortex solves a basic problem: how to analyze the visual scene in detail in the central part and much more crudely in the periphery. In the retina, which has the same problem, for obvious optical reasons the number of millimeters corresponding to a degree of visual field is constant. The retina handles the central areas in great detail by having huge numbers of ganglion cells, each subserving a tiny area of central visual field; the layer of ganglion cells in the central part of the retina is thick, whereas in the outlying parts of the retina it is very thin. The cortex, in contrast, seems to want to be uniform in thickness everywhere. Here there are none of the optical constraints imposed on the retina, and so area is simply allotted in amounts corresponding to the problem at hand.

The machinery in any square millimeter of cortex is presumably about the same as in any other. A few thousand geniculate fibers enter such a region, the cortex does its thing and perhaps 50,000 fibers leave—whether a small part of the visual world is represented in great detail or a larger part in correspondingly less detail. The uniformity of the cortex is suggested, as we indicated at the outset, by the appearance of stained sections. It is compellingly confirmed when we examine the architecture further, looking specifically at orientation and at ocular dominance.

For orientation we inquire about groupings of cells just as we did with field position, looking first at two cells sitting side by side. Two such cells almost invariably have the same optimal stimulus orientation. If the electrode is inserted in a direction perpendicular to the surface, all the cells along the path of penetration have identical or almost identical orientations (except for the cells deep in layer IV, which have no optimal orientation at all). In two perpendicular penetrations a millimeter or so apart, however, the two orientations observed are usually different. The cortex must therefore be subdivided by some kind of vertical partitioning into regions of constant receptive-field orientation. When we came on this system almost 20 years ago, it intrigued us because it fitted so well with the hierarchical schemes we had proposed to explain how complex cells are supplied by inputs from simple cells: the circuit diagrams involve connections between cells whose fields cover the same part of the visual world and that respond to the same line orientation. It seemed eminently reasonable that strongly inter-



GROUPING OF CELLS according to ocular dominance was revealed by physiological studies. In one typical vertical penetration of the cortex (1) a microelectrode encounters only cells that respond preferentially to the left eye (L_r) and, in layer IV, cells that respond only to the left eye (L); in another vertical penetration (2) the cells all have right-eye dominance (R_r) or, in layer IV, are driven exclusively by the right eye (R). In an oblique penetration (3) there is a regular alternation of dominance by one eye or the other eye. Repeated penetrations suggest that the cortex is subdivided into regions with a cross-sectional width of about .4 millimeter and with walls perpendicular to the cortical surface and layers: the **ocular-dominance columns**.

connected cells should be grouped together.

If the cortex is diced up into small regions of constant receptive-field orientation, can one say anything more about the three-dimensional shape of the regions than that their walls are perpendicular to the surface? Are neighboring regions related in any systematic way or are regions subserving all the possible orientations scattered over the cortex at random? We began to study these questions simply by penetrating the cortex obliquely or parallel to the surface. When we first did this experiment in about 1961, the result was so surprising that we could hardly believe it. Instead of a random assortment of successive orientations there was an amazing orderliness. Each time the electrode moved forward as little as 25 or 50 micrometers (thousandths of a millimeter) the optimal orientation changed by a small step, about 10 degrees on the average; the steps continued in the same direction, clockwise or counterclockwise, through a total angle of anywhere from 90 to 270 degrees. Occasionally such a sequence would reverse direction suddenly, from a clockwise progression to a counterclockwise one or vice versa. These reversals were unpredictable, usually coming after steady progressions of from 90 to 270 degrees.

Since making this first observation we have seen similar order in almost every monkey. Either there is a steady progression in orientation or, less frequently, there are stretches in which orientation stays constant. The successive changes in orientation are small enough so that it is hard to be sure that the regions of constant orientation are finite in size; it could be that the optimal orientation changes in some sense continuously as the electrode moves along the cortex.

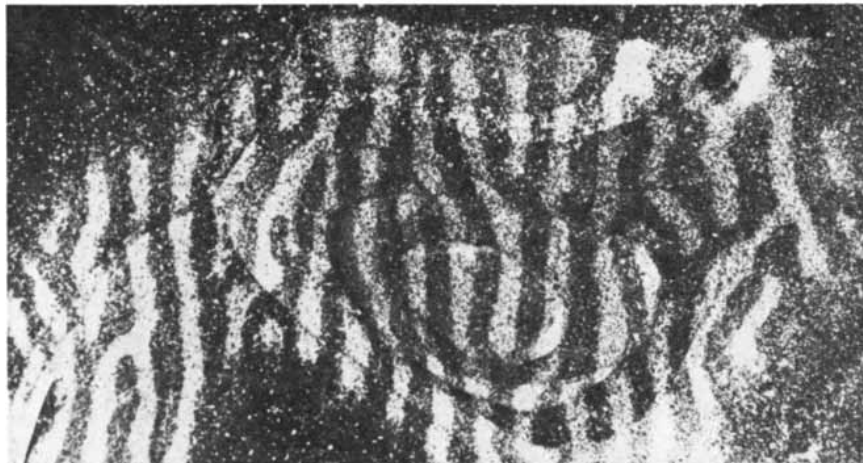
We became increasingly interested in the three-dimensional shape of these regional subdivisions. From considerations of geometry alone the existence of small or zero changes in every direction during a horizontal or tangential penetration points to parallel slabs of tissue containing cells with like orientation specificity, with each slab perpendicular to the surface. The slabs would not necessarily be planar, like slices of bread; seen from above they might well have the form of swirls, which could easily explain the reversals in the direction of orientation changes. Recording large numbers of cells in several parallel electrode penetrations seemed to confirm this prediction, but it was hard to examine more than a tiny region of brain with the microelectrode.

Fortunately an ideal anatomical method was invented at just the right time for us. This was the 2-deoxyglucose technique for assessing brain activity, devised by Louis Sokoloff and his group

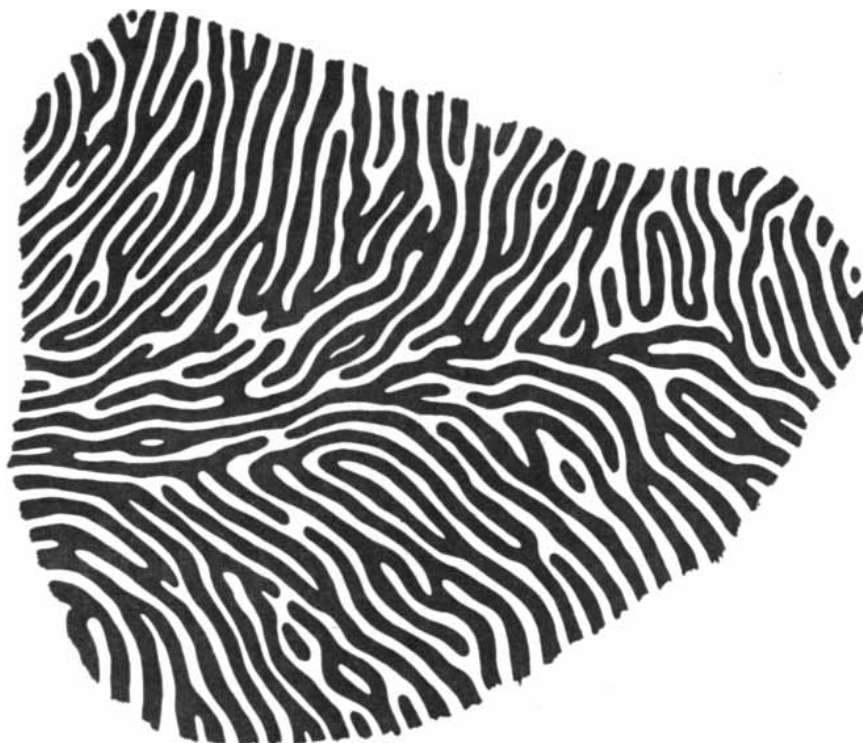
at the National Institute of Mental Health and described elsewhere in this issue [see "The Chemistry of the Brain," by Leslie L. Iversen, page 134]. The method capitalizes on the fact that brain cells depend mainly on glucose as a source of metabolic energy and that the closely similar compound 2-deoxyglucose can to some extent masquerade as glucose. If deoxyglucose is injected into an animal, it is taken up actively by neurons as though it were glucose; the more

active the neuron, the greater the uptake. The compound begins to be metabolized, but for reasons best known to biochemists the sequence stops with a metabolite that cannot cross the cell wall and therefore accumulates within the cell.

The Sokoloff procedure is to inject an animal with deoxyglucose that has been labeled with the radioactive isotope carbon 14, stimulate the animal in a way calculated to activate certain neurons



ANATOMICAL CONFIRMATION of ocular-dominance columns came from various staining methods and from axonal-transport autoradiographs such as those shown in color on page 151. This composite autoradiograph visualizing the pattern over an area some 10 millimeters wide was made by cutting out and pasting together the regions representing layer IV in a number of parallel sections: the one in bottom illustration on page 151 and others at different depths.



RECONSTRUCTION of the ocular-dominance pattern over the entire exposed part of the right primary visual cortex was made by the authors and Simon LeVay from a series of sections stained by a reduced-silver method he developed. The left-hand margin is at the medial edge of occipital lobe, where cortex folds downward; pattern is enlarged about six diameters.

and then immediately examine the brain for radioactivity, which reveals active areas where cells will have taken up more deoxyglucose than those in quiescent areas. The usual way of examining the brain for this purpose is to cut very thin slices of it (as one would for microscopic examination) and press them against a photographic plate sensitive to the radioactive particles. When the film is developed, any areas that were in contact with radioactive material are seen as dark masses of developed silver grains. Together with Michael P. Stryker we adapted the Sokoloff method to our problem, injecting an anesthetized animal with deoxyglucose and then moving a pattern of black and white vertical stripes back and forth 1.5 meters in front of the animal for 45 minutes. We then cut the brain into slices, either perpendicular to the surface of the cortex or parallel to it.

The autoradiographs quickly confirmed the physiological results. Sections cut perpendicular to the surface showed narrow bands of radioactivity about every 570 micrometers (roughly half a millimeter), extending through the full thickness of the cortex. Evidently these were the regions containing cells responsive to vertical lines. The deep

part of layer IV was uniformly radioactive, as was expected from the fact that the cells in the layer have circularly symmetrical receptive fields and show no orientation selectivity.

Sections cut parallel to the surface showed an unexpectedly complex set of periodically spaced bands, often swirling, frequently branching and rejoining, only here and there forming regular parallel slabs. What was particularly striking was the uniformity of the distance from one band to the next over the entire cortex. This fitted perfectly with the idea of a uniform cortex. Moreover, the distance between stripes fitted well with the idea that the cortical machinery must repeat itself at least every millimeter. If the distance were, for example, 10 millimeters from vertical through 180 degrees and back to vertical, sizable parts of the visual field would lack cells sensitive to any given orientation, making for a sketchy and extremely bizarre representation of the visual scene.

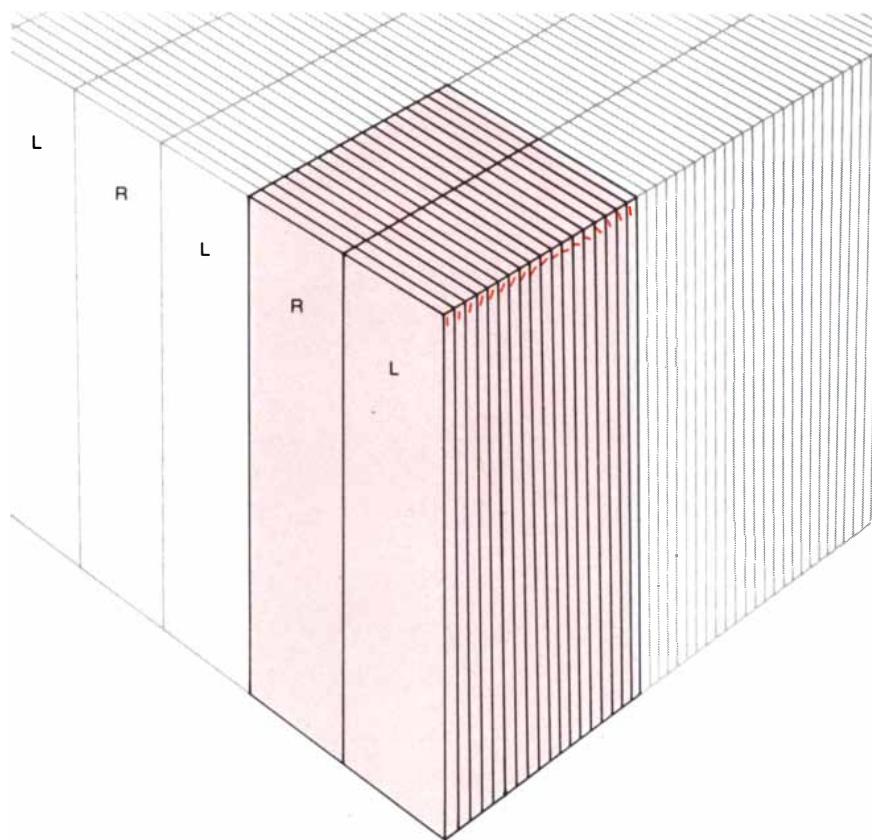
The final variable whose associated architecture needs to be considered is eye preference. In microelectrode studies neighboring cells proved almost invariably to prefer the same eye. If in vertical penetrations the first cell we en-

countered preferred the right eye, then so did all the cells, right down to the bottom of layer VI; if the first cell preferred the left eye, so did all the rest. Any penetration favored one eye or the other with equal probability. (Since the cells of layer IV are monocular, there it was a matter not of eye preference but of eye monopoly.) If the penetration was oblique or horizontal, there was an alternation of left and right preferences, with a rather abrupt switchover about every half millimeter. The cortex thus proved to be diced up into a second set of regions separated by vertical walls that extend through the full cortical thickness. The ocular-dominance system was apparently quite independent of the orientation system, because in oblique or tangential penetrations the two sequences had no apparent relation to each other.

The basis of these ocular-dominance columns, as they have come to be called, seems to be quite simple. The terminals of geniculate fibers, some subserving the left eye and others the right, group themselves as they enter the cortex so that in layer IV there is no mixing. This produces left-eye and right-eye patches at roughly half-millimeter intervals. A neuron above or below layer IV receives connections from that layer from up to about a millimeter away in every direction. Probably the strongest connections are from the region of layer IV closest to the neuron, so that it is presumably dominated by whichever eye feeds that region.

Again we were most curious to learn what these left-eye and right-eye regions might look like in three dimensions; any of several geometries could lead to the cross-sectional appearance the physiology had suggested. The answer first came from studies with the silver-degeneration method for mapping connections, devised by Walle J. H. Nauta of the Massachusetts Institute of Technology. Since then we have found three other independent anatomical methods for demonstrating these columns.

A particularly effective method (because it enables one to observe in a single animal the arrangement of columns over the entire primary visual cortex) is based on the phenomenon of axonal transport. The procedure is to inject a radioactively labeled amino acid into an area of nervous tissue. A cell body takes up the amino acid, presumably incorporates it into a protein and then transports it along the axon to its terminals. When we injected the material into one eye of a monkey, the retinal ganglion cells took it up and transported it along their axons, the optic-nerve fibers. We could then examine the destinations of these fibers in the lateral geniculate nuclei by coating tissue slices with a silver emulsion and developing the emulsion; the radioactive label showed up clearly in



BLOCK OF CORTEX about a millimeter square and two millimeters deep (light color) can be considered an elementary unit of the primary visual cortex. It contains one set of orientation slabs subserving all orientations and one set of ocular-dominance slabs subserving both eyes. The pattern is reiterated throughout the primary visual area. The placing of the boundaries (at the right or the left eye, at a vertical, horizontal or oblique orientation) is arbitrary; representation of the slabs as flat planes intersecting at right angles is an oversimplification.

the three complementary layers of the geniculate on each side.

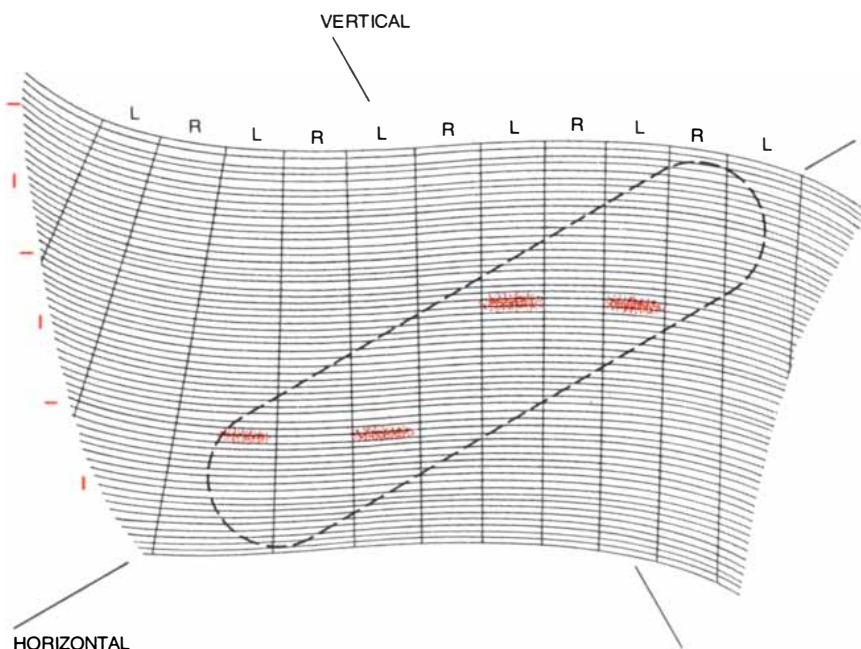
This method does not ordinarily trace a path from one axon terminal across a synapse to the next neuron and its terminals, however, and we wanted to follow the path all the way to the cortex. In 1971 Bernice Grafstein of the Cornell University Medical College discovered that after a large enough injection in the eye of a mouse some of the radioactive material escaped from the optic-nerve terminals and was taken up by the cells in the geniculate and transported along their axons to the cortex. We had the thought that a similarly large injection in a monkey, combined with autoradiography, might demonstrate the geniculate terminals from one eye in layer IV of the visual cortex.

Our first attempt yielded dismayingly negative results, with only faint hints of a few silver grains visible in layer IV. It was only after several weeks that we realized that by resorting to dark-field microscopy we could take advantage of the light-scattering properties of silver grains and so increase the sensitivity of the method. We borrowed a dark-field condenser, and when we looked at our first slide under the microscope, there shining in all their glory were the periodic patches of label in layer IV [see top illustration on page 151].

The next step was to try to see the pattern face on by sectioning the cortex parallel to its surface. The monkey cortex is dome-shaped, and so a section parallel to the surface and tangent to layer IV shows that layer as a circle or an oval, while a section below layer IV shows it as a ring. By assembling a series of such ovals and rings from a set of sections one can reconstruct the pattern over a wide expanse of cortex.

From the reconstructions it was immediately obvious that the main overall pattern is one of parallel stripes representing terminals belonging to the injected eye, separated by gaps representing the other eye. The striping pattern is not regular like wallpaper. (We remind ourselves occasionally that this is, after all, biology!) Here and there a stripe representing one eye branches into two stripes, or else it ends blindly at a point where a stripe from the other eye branches. The irregularities are commonest near the center of gaze and along the line that maps the horizon. The stripes always seem to be perpendicular to the border between the primary visual cortex and its neighbor, area 18, and here the regularity is greatest. Such general rules seem to apply to all macaque brains, although the details of the pattern vary from one individual to the next and even from one hemisphere to the other in the same monkey.

The width of a set of two stripes is constant, about .8 millimeter, over the



HYPOTHETICAL PATTERN OF CORTICAL ACTIVITY that might result from stimulation of the left eye with a single short horizontal line, placed in the upper left quadrant of the visual field, is shown by the colored patches on a diagram of an area of the right cortex, seen face on. The area receiving input from the object in the visual field is indicated by the broken black line. If ocular-dominance and orientation columns are arrayed as shown, activated cells will be those that respond optimally to approximately horizontal stimuli from the left eye.

entire primary visual cortex, once more emphasizing the uniformity of the cortex. Again the widths fit perfectly with the idea that all of the apparatus needed to look after an area the size of an aggregate field must be contained within any square millimeter of cortex. The two techniques, deoxyglucose labeling and amino acid transport, have the great advantage of being mutually compatible, so that we have been able to apply both together, one to mark orientation lines and the other to see the ocular-dominance columns. The number of brains examined so far is too small to justify any final conclusions, but the two systems appear to be quite independent, neither parallel nor at right angles but intersecting at random.

The function served by ocular-dominance columns is still a mystery. We know there are neurons with all grades of eye preference throughout the entire binocular part of the visual fields, and it may be that a regular, patterned system of converging inputs guarantees that the distribution will be uniform, with neither eye favored by accident in any one place. Why there should be all these grades of eye preference everywhere is itself not clear, but our guess is that it has something to do with stereoscopic depth perception.

Given what has been learned about the primary visual cortex, it is clear that one can consider an elementary piece of cortex to be a block about a millimeter square and two millimeters

deep. To know the organization of this chunk of tissue is to know the organization for all of area 17; the whole must be mainly an iterated version of this elementary unit. Of course the elementary unit should not be thought of as a discrete, separable block. Whether the set of orientation slabs begins with a slab representing a vertical orientation, an oblique one or a horizontal one is completely arbitrary; so too is whether an ocular-dominance sequence begins with a left-plus-right pair of dominance slabs or a right-plus-left pair. The same thing is true for a unit crystal of sodium chloride or for any complex repetitive pattern such as is found in wallpaper.

What, then, does the visual scene really look like as it is projected onto the visual cortex? Suppose an animal fixes its gaze on some point and the only object in the visual field is a straight line above and a bit to the left of the point where the gaze is riveted. If each active cell were to light up, and if one could stand above the cortex and look down at it, what would the pattern be? To make the problem more interesting, suppose the pattern is seen by one eye only. In view of the architecture just described the pattern turns out to be not a line but merely a set of regularly spaced patches [see illustration above]. The reasoning can be checked directly by exposing a monkey with one eye closed to a set of vertical stripes and making a deoxyglucose autoradiograph. The resulting pattern should not be a great surprise: it is a set of regularly spaced patches, which sim-

ply represents the intersection of the two sets of column systems. Imagine the surprise and bewilderment of a little green man looking at such a version of the outside world!

Why evolution has gone to the trouble of designing such an elaborate architecture is a question that continues to fascinate us. Perhaps the most plausible notion is that the column systems are a solution to the problem of portraying more than two dimensions on a two-dimensional surface. The cortex is dealing with at least four sets of values: two for the x and y position variables in the visual field, one for orientation and one for the different degrees of eye preference. The two surface coordinates are used up in designating field position; the other two variables are accommodated by dicing up the cortex with subdivisions so fine that one can run through a complete set of orientations or eye preferences and meanwhile have a shift in visual-field position that is small with respect to the resolution in that part of the visual world.

The strategy of subdividing the cortex with small vertical partitions is certainly not limited to the primary visual area. Such subdivisions were first seen in the somatic sensory area by Vernon B. Mountcastle of the Johns Hopkins University School of Medicine about 10 years before our work in the visual area. In the somatic sensory area, as we point-

ed out above, the basic topography is a map of the opposite half of the body, but superimposed on that there is a two-fold system of subdivisions, with some areas where neurons respond to the movement of the joints or pressure on the skin and other areas where they respond to touch or the bending of hairs. As in the case of the visual columns, a complete set here (one area for each kind of neuron) occupies a distance of about a millimeter. These subdivisions are analogous to ocular-dominance columns in that they are determined in the first instance by inputs to the cortex (from either the left or the right eye and from either deep receptors or receptors in the upper skin layers) rather than by connections within the cortex, such as those that determine orientation selectivity and the associated system of orientation regions.

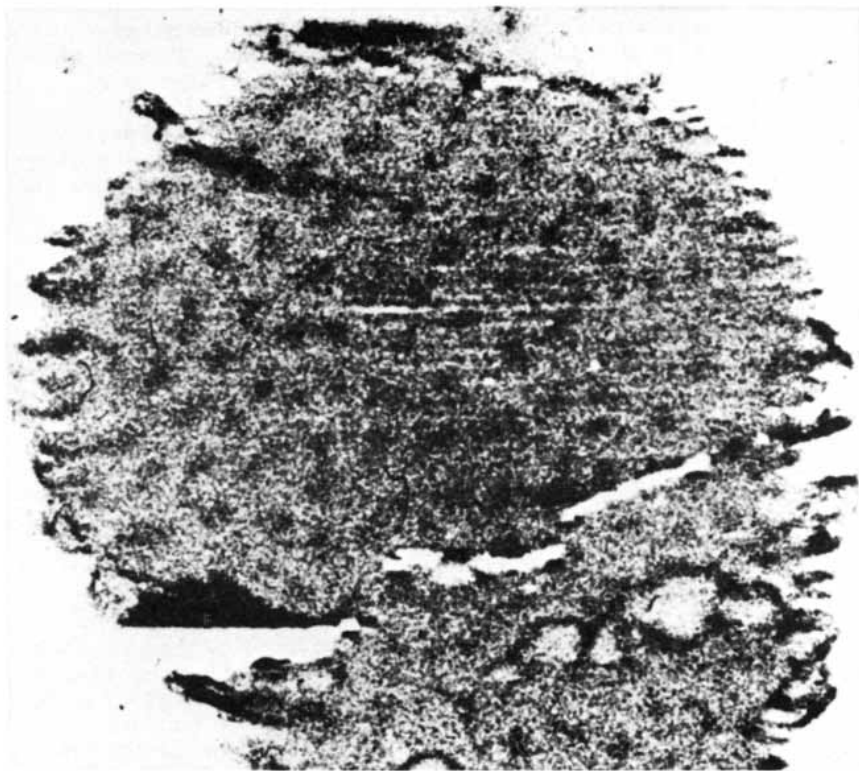
The columnar subdivisions associated with the visual and somatic sensory systems are the best-understood ones, but there are indications of similar vertical subdivisions in some other areas: several higher visual areas, sensory parietal regions recently studied by Mountcastle and the auditory region, where Thomas J. Imig, H. O. Adrián and John F. Brugge of the University of Wisconsin Medical School and their colleagues have found subdivisions in which the two ears seem alternately to add their information or to compete.

For most of these physiologically defined systems (except the visual ones) there are so far no anatomical correlates. On the other hand, in the past few years several anatomists, notably Edward G. Jones of the Washington University School of Medicine and Nauta and Patricia Goldman at M.I.T., have shown that connections from one region of the cortex to another (for example from the somatic sensory area on one side to the corresponding area on the other side) terminate in patches that have a regular periodicity of about a millimeter. Here the columns are evident morphologically, but one has no idea of the physiological interpretation. It is clear, however, that fine periodic subdivisions are a very general feature of the cerebral cortex. Indeed, Mountcastle's original observation of that feature may be said to supply a fourth profound insight into cortical organization.

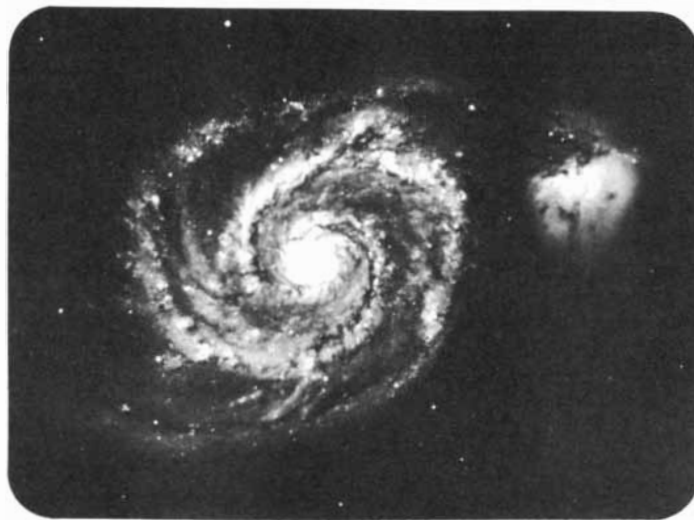
It would surely be wrong to assume that this account of the visual cortex in any way exhausts the subject. Color, movement and stereoscopic depth are probably all dealt with in the cortex, but to what extent or how is still not clear. There are indications from work we and others have done on depth and from work on color by Semir Zeki of University College London that higher cortical visual areas to which the primary area projects directly or indirectly may be specialized to handle these variables, but we are a long way from knowing what the handling involves.

What happens beyond the primary visual area, and how is the information on orientation exploited at later stages? Is one to imagine ultimately finding a cell that responds specifically to some very particular item? (Usually one's grandmother is selected as the particular item, for reasons that escape us.) Our answer is that we doubt there is such a cell, but we have no good alternative to offer. To speculate broadly on how the brain may work is fortunately not the only course open to investigators. To explore the brain is more fun and seems to be more profitable.

There was a time, not so long ago, when one looked at the millions of neurons in the various layers of the cortex and wondered if anyone would ever have any idea of their function. Did they all work in parallel, like the cells of the liver or the kidney, achieving their objectives by pure bulk, or were they each doing something special? For the visual cortex the answer seems now to be known in broad outline: Particular stimuli turn neurons on or off; groups of neurons do indeed perform particular transformations. It seems reasonable to think that if the secrets of a few regions such as this one can be unlocked, other regions will also in time give up their secrets.



ACTUAL PATTERN of cortical activity was elicited by exposing only the left eye to a set of vertical stripes. The deoxyglucose autoradiograph is of a tangential section in the outer layers of the cortex. The pattern of regularly spaced dark patches of radioactivity represents intersection of ocular-dominance and orientation systems. Magnification is about eight diameters.



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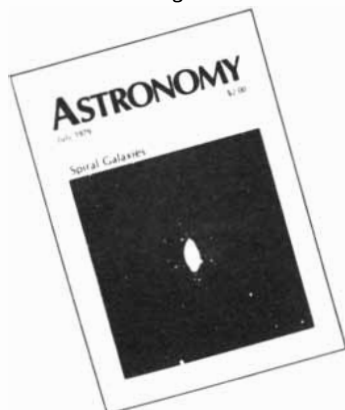
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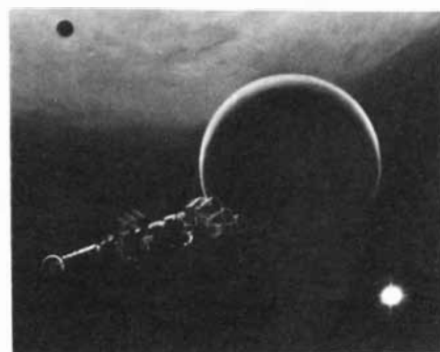
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