

6. MAGNIFICATION AND MODULES

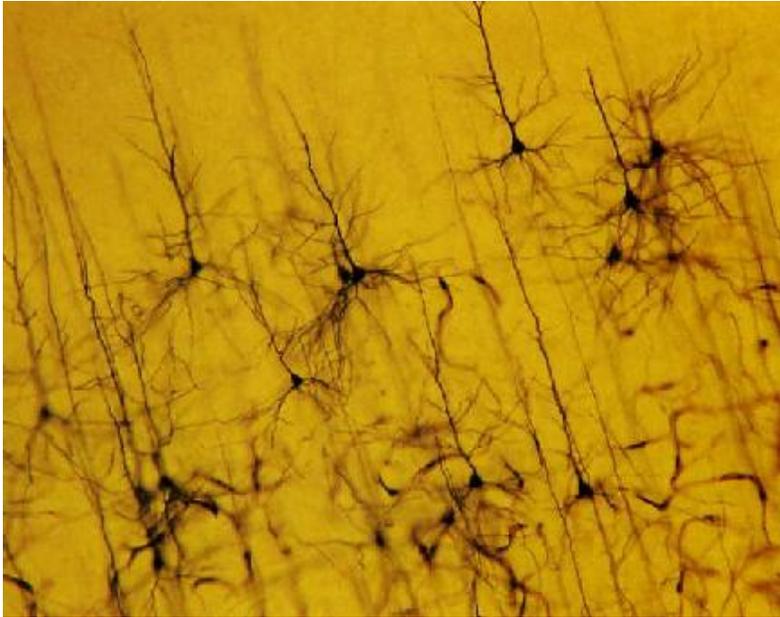
In the last chapter I emphasized the uniformity of the anatomy of the cortex, as it appears to the naked eye and even, with most ordinary staining methods, under the microscope. Now, on closer inspection, we have found anatomical uniformity prevailing in the topography of the ocular-dominance columns: the repeat distance, from left eye to right eye, stays remarkably constant as we go from the fovea to the far periphery of the binocular region. With the help of the deoxyglucose method and optical mapping techniques, we have found uniformity in the topography of the orientation columns as well.

This uniformity came at first as a surprise, because functionally the visual cortex is decidedly nonuniform, in two important respects. First, as described in Chapter 3, the receptive fields of retinal ganglion cells in or near the fovea are much smaller than those of cells many degrees out from the fovea. In the cortex, the receptive field of a typical complex upper-layer cell in the foveal representation is about one-quarter to one-half a degree in length and width. If we go out to 80 or 90 degrees, the comparable dimensions are more like 2 to 4 degrees—a ratio, in area, of about 10 to 30.

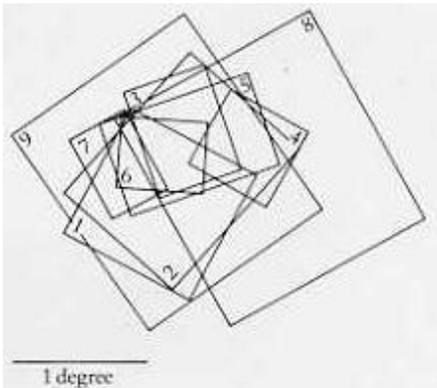
The second kind of nonuniformity concerns *magnification*, defined in 1961 by P. M. Daniel and David Whitteridge as the distance in the cortex corresponding to a distance of i degree in the visual field. As we go out from the fovea, a given amount of visual field corresponds to a progressively smaller and smaller area of cortex: the magnification decreases. If, near the fovea, we move 1 degree in the visual field, we travel about 6 millimeters on the cortex; 90 degrees out from the fovea, 1 degree in the visual field corresponds to about 0.15 millimeter along the cortex. Thus magnification in the fovea is roughly thirty-six times larger than in the periphery. Both these nonuniformities make sense—and for the same reason—namely, that our vision gets progressively cruder with distance from the fovea. Just try looking at a letter at the extreme left of this page and guessing at any letter or word at the extreme right. Or look at the word *progressively*: if you fix your gaze on the p at the beginning, you may just barely be able to see the y at the end, and you will certainly have trouble with the e or the / before the y. Achieving high resolution in the foveal part of our visual system requires many cortical cells per unit area of visual field, with each cell taking care of a very small domain of visual field.

THE SCATTER AND DRIFT OF RECEPTIVE FIELDS

How, then, can the cortex get away with being so uniform anatomically? To understand this we need to take a more detailed look at what happens to receptive-field positions as an electrode moves through the cortex. If the electrode is inserted into the striate cortex exactly perpendicular to the surface, the receptive fields of cells encountered as the tip moves forward are all located in almost the same place, but not exactly: from cell to cell we find variations in position, which seem to be random and are small enough that some overlap occurs between almost every field and the next one, as shown in the illustration at the top of next page.



A single module of the type discussed in this chapter occupies roughly the area shown in this photograph of a Golgi-stained section through visual cortex. The Golgi method stains only a tiny fraction of the nerve cells in any region, but the cells that it does reveal are stained fully or almost so; thus one can see the cell body, dendrites, and axon.

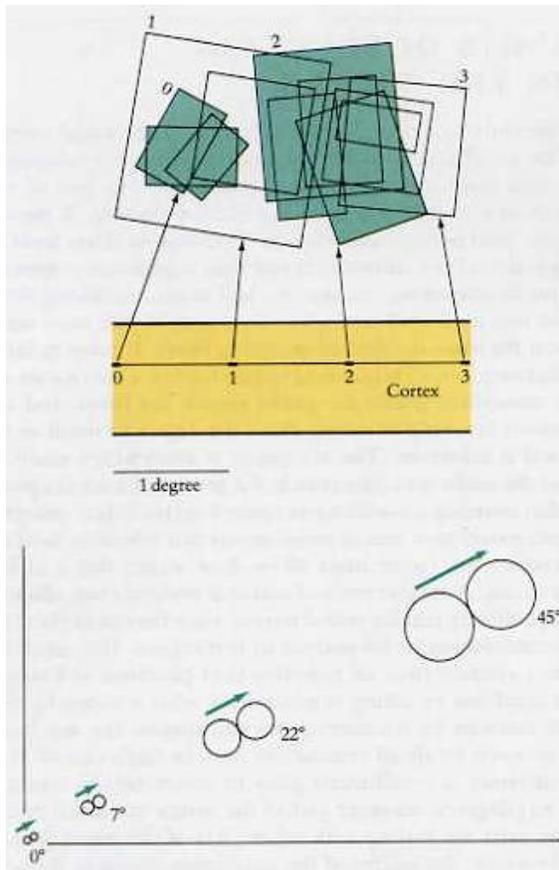


These nine receptive fields were mapped in a cat striate cortex in a single microelectrode penetration made perpendicular to the surface. As the electrode descends, we see random scatter in receptive-field position and some variation in size but see no overall tendency for the positions to change.

The sizes of the fields remain fairly constant in any given layer but differ markedly from one layer to another, from very small, in layer 4C, to large, in layers 5 and 6. Within any one layer, the area of visual field occupied by ten or twenty successively recorded receptive fields is, because of this random scatter, about two to four times the area occupied by any single field. We call the area occupied by a large number of superimposed fields in some layer and under some point on the cortex the *aggregate receptive field* of that point in that layer. In any given layer, the aggregate field varies, for example in layer 3, from about 30 minutes of arc in the foveal region to about 7 or 8 degrees in the far periphery.

Now suppose we insert the electrode so that it moves horizontally along any one layer,

say layer 3. Again, as cell after cell is recorded, we see in successive receptive fields a chaotic variation in position, but superimposed on this variation we now detect a steady drift in position. The direction of this drift in the visual field is, of course, predictable from the systematic map of visual fields onto cortex. What interests us here is the amount of drift we see after 1 millimeter of horizontal movement along the cortex. From what I have said about variation in magnification, it will be clear that the distance traversed in the visual field will depend on where in the cortex we have been recording— whether we are studying a region of cortex that represents the foveal region, the far periphery of the visual field, or somewhere between. The rate of movement through the visual field will be far from constant. But the movement turns out to be very constant relative to the size of the receptive fields themselves. One millimeter on the cortex everywhere produces a movement through the visual field that is equal to about half the territory occupied by the aggregate receptive field—the smear of fields that would be found under a single point in the region. Thus about 2 millimeters of movement is required to get entirely out of one part of the visual field and into the next, as shown in the illustration below (top one). This turns out to be the case wherever in area 17 we record. In the fovea, the receptive fields are tiny, and so is the movement in the visual field produced by a 2-millimeter movement along the cortex: in the periphery, both the receptive fields and the movements are much larger, as illustrated in the lower figure on this page.



In the course of a long penetration parallel to the cortical surface in a cat, receptive fields drifted through

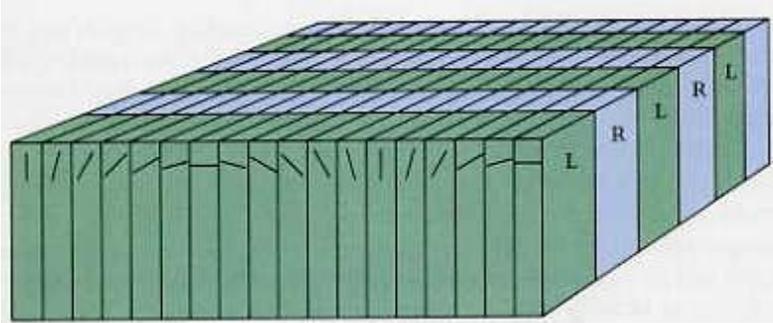
the visual field. The electrode traveled over 3 millimeters and recorded over sixty cells, far too many to be shown in a figure like this. I show instead only the positions of four or five receptive fields mapped in the first tenth of each millimeter, ignoring the other nine tenths. For the parts of the penetration drawn with a thick pen in the lower half of the diagram (numbered 0, 1, 2, and 3), the receptive fields of cells encountered are mapped in the upper part. Each group is detectably displaced to the right in the visual field relative to the previous group. The fields in group 2 do not overlap with those in group 0, and group-3 fields do not overlap with group-1 fields; in each case the cortical separation is 2 millimeters.

In a macaque monkey, the upper-layer receptive fields grow larger as eccentricity increases from the fovea (0 degrees). Also growing by an equal amount is the distance the receptive fields move in the visual field when an electrode moves 2 millimeters along the cortex parallel to the surface.

UNITS OF FUNCTION IN THE CORTEX

We must conclude that any piece of primary visual cortex about 2 millimeters by 2 millimeters in surface area must have the machinery to deal completely with some particular area of visual field—an area of visual field that is small in or near the fovea and large in the periphery. A piece of cortex receiving input from perhaps a few tens of thousands of fibers from the geniculate first operates on the information and then supplies an output carried by fibers sensitive to orientation, movement, and so on, combining the information from the two eyes: each such piece does roughly the same set of operations on about the same number of incoming fibers. It takes in information, highly detailed over a small visual-field terrain for fovea but coarser and covering a larger visual-field terrain for points outside the fovea, and it emits an output—without knowing or caring about the degree of detail or the size of the visual field it subserves. The machinery is everywhere much the same. That explains the uniformity observed in the gross and microscopic anatomy. The fact that covering a 2-millimeter span of cortex is just enough to move you into a completely new area of retina means that whatever local operations are to be done by the cortex must all be done within this 2 millimeter by 2 millimeter chunk. A smaller piece of cortex is evidently not adequate to deal with a correspondingly smaller retinal terrain, since the rest of the 2-millimeter piece is also contributing to the analysis of that region. This much is obvious simply from a consideration of receptive-field positions and sizes, but the point can be amplified by asking in more detail what is meant by analysis and operation. We can start by considering line orientation. For any region in the visual field, however small, all orientations must be taken care of. If in analyzing a piece of retina, a 2-millimeter piece of cortex fails to take care of the orientation +45 degrees, no other part of the cortex can make up the deficit, because other parts are dealing with other parts of the visual field. By great good luck, however, the widths of the orientation stripes in the cortex, 0.05 millimeter, are just small enough that with 180 degrees to look after in 10-degree steps, all orientations can be covered comfortably, more than twice over, in 2 millimeters. The same holds for eye dominance: each eye requires 0.5 millimeter, so that 2 millimeters is more than enough. In a 2-millimeter block, the cortex seems to possess, as indeed it must, a complete set of machinery. Let me hasten to add that the 2-millimeter distance is a property not so much of area 17 as of layer 3 in area 17. In layers 5 and 6, the fields and the scatter are twice the size, so that a block roughly 4 millimeters by 4 millimeters would presumably be needed to do everything layers 5 and 6 do, such as constructing big complex fields with

rather special properties. At the other extreme, in layer 4C, fields and scatter are far smaller, and the corresponding distance in the cortex is more like 0.1 to 0.2 millimeter. But the general argument remains the same, unaffected by the fact that several local sets of operations are made on any given region of visual field in several different layers—that is, despite the fact that the cortex is several machines in one.



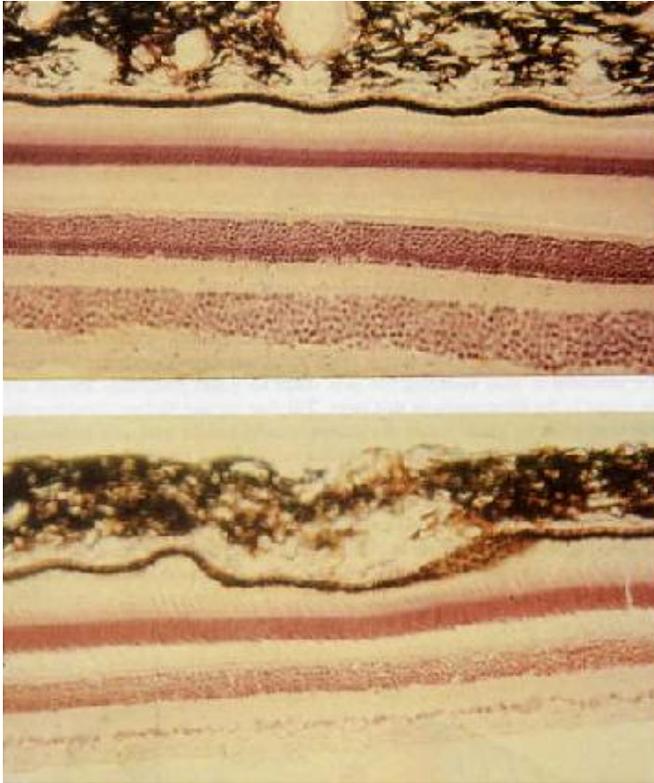
We call this our "ice cube model" of the cortex. It illustrates how the cortex is divided, at one and the same time, into two kinds of slabs, one set for ocular dominance (left and right) and one set for orientation. The model should not be taken literally: Neither set is as regular as this, and the orientation slabs especially are far from parallel or straight. Moreover, they do not seem to intersect in any particular angle—certainly they are not orthogonal, as shown here.

All this may help us to understand why the columns are not far more coarse. Enough has to be packed into a 2 millimeter by 2 millimeter block to include all the values of the variables it deals with, orientation and eye preference being the ones we have talked about so far. What the cortex does is map not just two but many variables on its two-dimensional surface. It does this by selecting as the basic parameters the two variables that specify the visual field coordinates (distance out and up or down from the fovea), and on this map it engrafts other variables, such as orientation and eye preference, by finer subdivisions. We call the 2 millimeter by 2 millimeter piece of cortex a module. To me, the word seems not totally suitable, partly because it is too concrete: it calls up an image of a rectangular tin box containing electronic parts that can be plugged into a rack beside a hundred other such boxes. To some extent that is indeed what we want the word to convey, but in a rather loose sense. First, our units clearly can start and end anywhere we like, in the orientation domain. They can go from vertical to vertical or -85 to +95 degrees, as long as we include all orientations at least once. The same applies to eye preference: we can start at a left-eye, right-eye border or at the middle of a column, as long as we include two columns, one for each eye. Second, as mentioned earlier, the size of the module we are talking about will depend on the layer we are considering. Nevertheless, the term does convey the impression of some 500 to 1000 small machines, any of which can be substituted for any other, provided we are ready to wire up 10,000 or so incoming wires and perhaps 50,000 outgoing ones! Let me quickly add that no one would suppose that the cortex is completely uniform from fovea to far periphery. Vision varies with visual-field position in several ways other than acuity. Our color abilities fall off with distance, although perhaps not very steeply if we compensate for magnification by making the object we are viewing bigger with

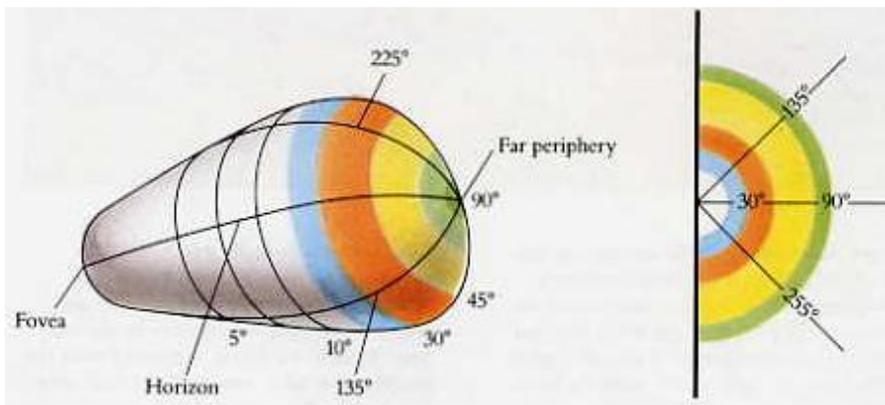
increasing distance from the fovea. Movement is probably better detected in the periphery, as are very dim lights. Functions related to binocular vision must obviously fall off because beyond 20 degrees and up to 80 degrees, ipsilateral-eye columns get progressively narrower and contralateral ones get broader; beyond 80 degrees the ipsilateral ones disappear entirely and the cortex becomes monocular. There must be differences in circuits to reflect these and doubtless other differences in our capabilities. So modules are probably not all exactly alike.

DEFORMATION OF THE CORTEX

We can get a deeper understanding of the geometry of the cortex by comparing it with the retina. The eye is a sphere, and that is consequently the shape of the retina, for purely optical reasons. A camera film can be flat because the angle taken in by the system is, for an average lens, about 30 degrees. A fish-eye camera lens encompasses a wider angle, but it distorts at the periphery. Of course, bowl-shaped photographs would be awkward—flat ones are enough of a pain to store. For the eye, a spherical shape is ideal, since a sphere is compact and can rotate in a socket, something that a cube does with difficulty! With a spherical eye, retinal magnification is constant: the number of degrees of visual field per millimeter of retina is the same throughout the retina—3.5 degrees per millimeter in human eyes. I have already mentioned that ganglion-cell receptive-field centers are small in and near the fovea and grow in size as distance from fovea increases, and accordingly we should not be surprised to learn that many more ganglion cells are needed in a millimeter of retina near the fovea than are needed far out. Indeed, near the fovea, ganglion cells are piled many cells high, whereas the cells farther out are spread too thin to make even one continuous layer, as the photographs at the top on the next page show. Because the retina has to be spherical, its layers cannot be uniform. Perhaps that is part of the reason for the retina's not doing more information processing than it does. The layers near the fovea would have to be much too thick. The cortex has more options. Unlike the retina, it does not have to be spherical; it is allowed simply to expand in its foveal part, relative to the periphery. It presumably expands enough so that the thickness—and incidentally the column widths and everything else—remains the same throughout.



In contrast to those of the cortex, the layers of the retina are far from constant in thickness. In both monkey and human the ganglion-cell layer near the fovea (bottom layer, top photograph) is many cell bodies thick, perhaps eight or ten, whereas far in the periphery, say 70 to 80 degrees out, (bottom photograph) there are too few ganglion cells to make one layer. This should be no surprise since foveal ganglion-cell field centers are tiny; they are larger in the periphery (just as in the cortex). Thus in the fovea, compared with the periphery, it takes more cells to look after a unit area of retina.



In the somatosensory cortex the problems of topography can become extreme to the point of absurdity. The cortex corresponding to the skin covering the hand, for example, should have basically a glove shape, with distortions over and above that to allow for the much greater sensory capacities of the finger tips, as compared with the palm or back of the hand. Such a distortion is analogous to the distortion of the foveal projections relative to the periphery, to allow for its greater acuity. Would the hand area of the cortex—if we modeled it in rubber and then stood inside and blew gently to get rid of the artificial creases—really resemble a glove? Probably not. Determining the map of the somatosensory cortex has turned out to be a daunting task. The results so far suggest that the predicted shape is just too bizarre; instead, the surface is cut up into manageable pieces as if with scissors, and pasted back together like a quilt so as to approximate a flat surface.

How does this affect the overall shape of the striate cortex? Although I have repeatedly called the cortex a plate, I have not necessarily meant to imply that it is a plane. If there were no distortion at all in shape, the striate cortex would be a sphere, just as the eyeball is and just as any map of the earth, if undistorted, must be. (Strictly, of course, the striate cortex on one side maps about half of the back halves of the two eyes, or about a quarter-sphere.) In stretching, so as to keep thickness constant and yet manage many more messages from the crowded layers of ganglion cells at the fovea, the cortex becomes distorted relative to the spherical surface that it otherwise would approximate. If we unfold and smooth out the creases in the cortex, we discover that it is indeed neither spherical nor flat; it has the shape of a very distorted quarter-sphere, rather like a pear or an egg. This result was predicted in 1962 by Daniel and Whitteridge, who determined experimentally the magnification in area 17 as a function of distance from the to veal representation, as mentioned on page 1, and used the result to calculate the three-dimensional shape. They then made a rubber model of the cortex from serial histological sections and literally unfolded it, thus verifying the pear shape they had predicted. We can see the shape in the illustration on the previous page. Till then no one had reasoned out the

question so as to predict that the cortex would unfold into any reasonable shape, nor, to my knowledge, had anyone realized that for any area of cortex, some shape or other must exist whose configuration should follow logically from its function. Presumably the folds, which must be smoothed out (without stretching or tearing) to get at the essential shape, exist because this large, distorted quarter-sphere must be crumpled to fit the compact box of the skull. The foldings may not be entirely arbitrary: some of the details are probably determined so as to minimize the lengths of cortico-cortical connections. In the somatosensory cortex the problems of topography can become extreme to the point of absurdity. The cortex corresponding to the skin covering the hand, for example, should have basically a glove shape, with distortions over and above that to allow for the much greater sensory capacities of the finger tips, as compared with the palm or back of the hand. Such a distortion is analogous to the distortion of the foveal projections relative to the periphery, to allow for its greater acuity. Would the hand area of the cortex—if we modeled it in rubber and then stood inside and blew gently to get rid of the artificial creases—really resemble a glove? Probably not. Determining the map of the somatosensory cortex has turned out to be a daunting task. The results so far suggest that the predicted shape is just too bizarre; instead, the surface is cut up into manageable pieces as if with scissors, and pasted back together like a quilt so as to approximate a flat surface.