The Functional Organization of Projections from Striate to Prestriate Visual Cortex in the Rhesus Monkey

S. M. Zeki

Department of Anatomy, University College London, London, WC1E 6BT, England

It is now well established that two of the major functions of the primary visual cortex (area 17) in the rhesus monkey are to bring the input of the two eyes together and to analyze the visual fields in detail for retinal contour (Hubel and Wiesel 1968). If one were to study the distribution of the efferent cortical projections from area 17, one might well suppose that another one of its major functions might be to segregate out the information coming over the retinogeniculate pathways and parcel this information out to different cortical areas for further analysis. Powerful evidence for such a supposition would be available if it could be shown that the distinct cortical areas to which the primary visual cortex projects have different populations of functional cell types. In a sense, this question is related to another question that has long excited the interest of neurologists: To what extent is there a division of labor within the visual cortex for handling information relating to different aspects of the visual environment? Although the evidence available is far from complete and certainly does not allow us to reach definitive conclusions, our understanding of the anatomical connections of the areas receiving direct inputs from area 17 has increased considerably over the past few years. Hand in hand with this has come an increased knowledge of the functional properties of the cells in these different areas, and this evidence has tended to suggest, but by no means proves, that there is indeed a concentration of different cell types in the different cortical areas and that, consequently, these different cortical areas may be specialized to handle different types of visual information.

PARALLEL AND INDEPENDENT EFFERENT OUTPUTS FROM AREA 17

Area 17 is surrounded by a wide cortical zone, commonly known as the prestriate cortex. There are no obvious cytoarchitectonic subdivisions within this prestriate cortex, but it has been customary since the time of Brodmann (1905) to subdivide it into two cytoarchitectonic fields, 18 and 19 (Fig. 1). Area 17 (VI) has five independent and parallel projections to the cytoarchitectonic area 18 (Fig. 2). The first of these is to V2, the second to V3, and the third to the cortex of the posterior bank of the superior temporal sulcus. Finally, there are projections, mainly, but not exclusively, from the region of foveal representation in area 17 to two further areas, V4 and V4a (Cragg 1969; Zeki 1969, 1971a) (see Figs. 1 and 2). As yet, we have no information concerning the laminar origins in area 17 of these different cortical output systems, and it is possible, and even likely, that different laminae in area 17 contribute differently to these efferent systems. But it would be difficult to suppose that the information carried out from area 17 in these distinct anatomical pathways is the same information. One way of studying this problem further, perhaps the simplest and most direct, is to record the responses of single cells or groups of cells in these cortical recipient zones, compare the responses of cells in one area with those in another, and determine whether there are any recognizable differences.

Recordings from Single Cells in Separate Prestriate Areas

The overall differences in the different prestriate areas can be illustrated by looking at a long penetration that starts through V2, crosses the lunate sulcus, passes through V4 and white matter, and finally terminates in the cortex of the posterior bank of the superior temporal sulcus (Fig. 3). In this way, the electrode passes through three of the five areas that receive direct inputs from area 17. In this particular penetration, all the cells illustrated in area V2 were binocularly driven complex cells with a well-defined orientational preference. However, such cells, which form the "ordinary cells of area 18" (Hubel and Wiesel 1970), constitute only about one-half of the population of cells in V2. There is, in addition, a heavy concentration of another type of cell, not found in area 17, which responds optimally when the visual stimulus falls on slightly disparate points in the two retinas (Hubel and Wiesel 1970). Other types of cells, including color-coded cells (S. M. Zeki, unpubl.), have also been found in V2, but these appear to be in a minority. One may conclude that among the functions emphasized in V2 is the analysis of the visual fields for binocular disparity.

1 Areas V2 and V3, as defined anatomically by degeneration methods, have also been called 18 and 19, but these are not to be confused with the cytoarchitectonic 18 and 19 of Brodmann (1905). However, to avoid confusion in this paper we shall simply speak of areas V2 and V3, although it should be understood that these terms are interchangeable with 18 and 19, as defined by degeneration techniques (Zeki 1969).
particular penetration (Fig. 3), all the cells illustrated were excited by blue light, or blue-green light, but, as we shall see below, there are several varieties of color-coded cells in V4.

Returning once again to the penetration illustrated in Figure 3, one notes another striking change in the properties of the neurons as the electrode hits the cortex of the posterior bank of the superior temporal sulcus. In this particular penetration, all the cells illustrated were of the directionally selective type, responding to motion in the appropriate direction irrespective of the form or orientation of the stimulus or its color. It is characteristic of the cells of this area that they are almost all responsive to movement, and a large majority are of the directionally selective type (Zeki 1974a), as opposed to the cells of area 17 in which directional selectivity is not nearly so prominent a feature (Hubel and Wiesel 1968). There are several subvarieties of such directionally selective cells: e.g., complex and hypercomplex cells, cells responding preferentially to small spots moved in the appropriate direction, and cells responding to motion in the appropriate direction regardless of the shape of the stimulus. There are also pandirectional cells, capable of responding to motion in any direction within the receptive field. We studied many, though not all, of the cells in this area that we have recorded from for wavelength preferences. In general, the cells appeared to respond autonomously regardless of wavelength, and once the appropriate stimulus was found, it seemed to make little difference what color the stimulus was.

Such cells would be well situated to analyze motion in all directions in the frontoparallel plane. But to analyze motion towards or away from the animal, a different type of cell would be needed. To date, we have found two major types of cells capable of signaling motion towards or away from the animal, both of which are located in the cortex of the posterior bank of the superior temporal sulcus (Zeki 1974b). In one type, also found in cat area 18 by Pettigrew (1973), the cells respond differently to stimulation of the two eyes (Fig. 4). A cell might

---

**Figure 1.** Tracings of horizontal sections taken through the brain of a rhesus monkey at the level indicated to show (A) the extent of area 18 as defined cytoarchitectonically by Brodmann (1905) and (B) the different anatomical zones within the cytoarchitectonic area 18 receiving direct inputs from the primary visual cortex (area 17). Only the posterior part of the brain is shown in these horizontal tracings. LS, lunate sulcus; STS, superior temporal sulcus.

---

**Figure 2.** Tracings of a horizontal section through the brain of a rhesus monkey to show, diagrammatically, the five independent and parallel projections from area 17 (continuous line in the cortex) to the prefrontal cortex. Exact topographic relations are not indicated in this figure. For further details, see text.
Figure 3. Diagrammatic reconstruction of a long penetration through the prestriate cortex of a rhesus monkey. The electrode entered the cortex through V2. For each cell, the receptive field position is separately indicated with reference to the fovea, which is indicated by the intersection of the short horizontal lines with the long, common vertical lines. Interrupted lines within the receptive field indicate the orientational preference of the cells. Where there is no such line, the cell had no orientational preference. The first cells recorded from (A, to left of figure) were in V2; they were all binocularly driven, orientation-selective cells, without any color preference. As the electrode crossed the lunate sulcus and hit V4 (B, in the center of figure), the cells recorded from were color-coded. In this penetration, all the cells, except cell 4, responded exclusively to blue light. Cell 4 had a wider spectral sensitivity, responding to green light as well (see text). The cells were binocularly driven. In the cortex of the posterior bank of the superior temporal sulcus, the character of the cells changed once again (C, to right of figure). The cells recorded from in this part of the penetration were binocularly driven, directionally selective cells for which the form, orientation or color of the stimulus were not relevant. Arrows indicate the preferred direction of motion of the stimulus.

B, blue; G, green; LS, lunate sulcus; STS, superior temporal sulcus.

Figure 4. (I) The response of a cell in the cortex of the posterior bank of the superior temporal sulcus to stimulation of the two eyes. The receptive field for the right eye is marked by the interrupted rectangle, that for the left eye by the solid rectangle. (A) Stimulation of the left eye by a slit of light moved in the direction marked by the arrow; (B) the same as in A but for the right eye. (C) The response to simultaneous movement in the null direction for each eye. (D) The response to simultaneous movement of a slit of light in the preferred direction for each eye. Duration of each trace is 5s. Left eye, l.e.; right eye, r.e. In II it is shown that when a point a, having its image at a and a', is displaced to b, having its image at b and b', the displacement is in opposite directions in each eye. For purposes of illustration, the distances on the retina are exaggerated in this figure.

(Reprinted, with permission, from Zeki 1974a,b.)
Figure 5. (I) The response of a binocularly driven, opposed movement complex cell in the cortex of the superior temporal sulcus to stimulation of the right eye. The cell gave a powerful response (A) when two dark edges were moved towards each other within the receptive field. Movement of the two edges away from each other (B) was ineffective, as was the movement of single, appropriately oriented edges or slits (C, D, F, G) or of two appropriately oriented slits moved in the appropriate direction. Orientation was critical (E). The size of the receptive field was 5° × 5° and was located in the lower, contralateral quadrant. Duration of each sweep was 4 s. (II) A diagram to show that when a large bar, aa', is moved to bb', the image will move in opposite directions in each eye. (Reprinted, with permission, from Zeki 1974b.)

 responded to motion from 3 o'clock to 9 o'clock for the right eye and from 9 o'clock to 3 o'clock for the left eye, thereby signaling motion towards the animal together with the changing disparity. The power of each of the two eyes to drive such a cell is not always equivalent, and for some of these changing disparity cells one eye may be more potent than the other in eliciting a response—presumably this mechanism aids in detecting motion towards the animal from the side.

Another type of cell capable of signaling motion towards or away from the animal is the opposed movement complex cell (Fig. 5). These cells, which may be driven either monocularly or binocularly, respond to two edges moving towards or away from each other, the orientation of the two edges being very critical. However when such a cell is driven monocularly, there is an ambiguity in the information that it may signal (Fig. 6); it could equally well signal information about an object at a fixed plane increasing.

Figure 6. Diagram to show that when a bar, aa', viewed monocularly, is displaced to bb', its image will move in opposite directions in each eye (A), and that the same motion across the retina will occur if instead of moving towards the eye, aa' becomes enlarged to bb': B (Reprinted, with permission, from Zeki 1974b.)
or decreasing in size. It is not known how the nervous system is able to differentiate between these two types of information.

Recordings from V4

Color-coded cells are in a minority in area 17 (Hubel and Wiesel 1968), and most of the color-coded cells to be found in area 17 are concentrated in the region of foveal representation (Dow and Gouras 1973). In contrast in V4, around 80% of the cells that we have successfully driven have been color-coded, and there are several categories of color-coded cells to be found in this area. One type, perhaps the simplest, responds to stimulation of a small part of the visual field with light of one wavelength, for example, red. In this case, there is no response to white light, even if it is more intense, or to other colors when radiometrically equated (Fig. 7). The cell illustrated in Figure 7 responded specifically to a red slit at a given orientation. But for many color-coded cells, orientation was not critical, nor was the direction of motion of the stimulus, and merely illuminating the receptive field with light of a particular color gave a powerful response. Although the absence of a response to white light immediately suggests that there is an opponent color input to such a cell, it is not always possible to obtain an off response to stimulation with other colors or inhibit the (frequently low) spontaneous discharge of the cell by stimulating the receptive field with light of other colors. For other cells, however, it is possible to study the opponent response. Such a cell might, for example, have a receptive field which is excitatory red on-center and inhibitory green off-center. Switching on the green light leads to a very striking suppression of the firing rate and switching it off causes a powerful off response.

Another type of cell behaves somewhat differently with regard to center and surround. Such a cell might, for example, be red on-center, giving a vigorous response when the stimulus is moved within the receptive field. However, invading the surround with red light might abolish the firing of the cell altogether. When such cells are orientation-selective, they are of the color-coded, "hypercomplex" type (Hubel and Wiesel 1968). When orientation is not critical, these cells show a remarkable similarity to the cells of the lateral geniculate nucleus (Wiesel and Hubel 1966), except that they are far more exigent in their requirements for specific wavelengths and are binocularly driven.

A cell in V4 can be even more exigent in the distribution of spectral sensitivity within its receptive field. Instead of the two spectral contributions being concentrated in one part of the receptive field, or the one spectral contribution in adjacent parts, the receptive field may be subdivided into antagonistic regions, with the regions having different, and opponent, color properties (see Fig. 3 in Zeki 1973). One color (e.g., green) may excite the center, and the opponent color (e.g., red) may have an inhibitory influence when flashed in the surround. Such cells may have various other distinctive features. The excitatory center may be completely enveloped by the opponent surround, or the opponent surround may be identifiable only around limited regions of the center. Where the excitatory center is surrounded on only two sides by antagonistic areas, these areas need not be equivalent in size. Finally, both the center and the surround may respond to the appropriate wavelength independently of contour, or contour may be critical for the center but not for the opponent color surround.

For another type of cell, the successive contrast cell, the most powerful response is obtained when the receptive field is flooded with light of a particular color and then changed to its opponent color. For example, the cell might respond to a change from green to red but not green to white, or red to green, or to green off, or to white on and white off.
The preceding gives a summary of the types of color-coded cells encountered in V4. Looking next at the spectral sensitivities of such cells, it is found that they vary from one cell to the next. Some "red cells," for example, respond over a range of 50 nm (from 670–620 nm), with a very sharp cut off at 600 nm. With such cells, it was usually not possible to elicit a response using other colors or white light at the highest intensities available. A "blue-green" cell may have a slightly wider spectral sensitivity, responding to light coming through interference filters between 560 nm and 480 nm. On the other hand, the spectral sensitivity of a "blue cell" may be narrower, the cell responding over a range of 40 nm. But cells with sharper spectral sensitivities have also been found. There are, for example, cells responding at 440 and 460 nm, in that end of the spectrum commonly known as violet. The cells give a powerful response at these wavelengths but respond weakly, if at all, to red or to blue. The violet cell (Fig. 8) is remarkable not only for displaying a sharp spectral curve, but also for having other specific attributes, namely, responding to a violet bar at a specific orientation.

We have also encountered color-coded cells responding to the extraspectral color magenta, or purple. The cell responded both to blue or to red but gave its optimal response to a superimposition of red and blue—an extraspectral color. It was fortunate that some of these cells had a high enough background activity for us to determine that green did provide an opponent input to these cells.

**Color-coding in Cortical Areas Surrounding V4**

The V4 area, as we have defined it elsewhere (Zeki 1971a), is flanked medially by V3 and laterally by V4a. We were naturally interested in exploring these two areas, especially the latter since it has an anatomical input closely similar to that of V4 (Zeki 1971a), to see whether there was any color-coding in either area.

**Responses of cells in area V3.** Area V3 lies immediately medial to V4. One is not always able to draw the boundary between V3 and V4 accurately in a Nissl-stained section. We were anxious to be secure in the knowledge that we were recording from area V3. The simplest way around this awkward problem was to section the corpus callosum several days prior to recording. The first area of degeneration in the anterior bank of the lunate sulcus defines the anterior boundary of area V3 (Cragg 1969; Zeki 1969, 1970). Electrode tracks within this area of degeneration or more medial to it were therefore accepted as being in area V3. In the 128 cells we have recorded from in area V3, we could not find any convincing example of color-coded cells. Complex cells formed the major segment of the population, followed by hypercomplex cells (Fig. 9). Cells were not studied for retinal disparity. Of course, the sampling was small, and a more extensive investigation may well show color-coded cells. Nevertheless, it seems clear that cells coded for color cannot be present in great concentrations in area V3.

**Responses of cells in V4a.** The cells of area V4a, lying lateral to V4 (Zeki 1971a), were difficult to drive, and many cells either habituated rapidly or had high spontaneous discharges, making their study difficult. Nevertheless, it was clear that these were visual cells, and it was only our own limitations that prevented us from driving them adequately. In addition to these vaguely driven cells, we succeeded in adequately driving 293 cells in this area, and the results are intriguing because many different varieties of cells may be found here. Complex cells, hypercomplex cells, cells having antagonistic surrounds but no orientational preference, pandirectional cells, cells responding to changes in intensity and color-coded cells were all encountered. Frequently, these different types of cells would all occur in the same penetration (Fig. 10), or a penetration would yield only one type of cell, for example, cells with orientational preferences (Fig. 11). Given the great variety of specific responses we have seen in this area, it is not clear what the
Figure 9. Reconstructions of penetrations through the depth and anterior bank of the lunate sulcus in a rhesus monkey at the level indicated. The dots in the cortex represent the degeneration following sectioning of the corpus callosum, and the most medial patch of degeneration (where the recordings were made) represents the anterior boundary of V3. Clearly the recordings were from V3. Conventions as in Figure 3. None of the 34 cells in the two penetrations was color-specific. The scale is 1".

function of this area may be. It certainly contains types of cells found in other cortical areas. From the point of view of color-coding, something on the order of 25% of the cells recorded from in this area have been color-specific, but there did not appear to be any striking differences between the color-coded cells of this area and the color-coded cells of V4. Despite having recorded from 293 cells in this cortical area, we are still uncertain of its status.

Differentiation between the Areas of the Prestriate Cortex

In summary, then, as one explores the five separate prestriate areas that receive a direct input from area 17, differences begin to appear. The cortex of the posterior bank of the superior temporal sulcus contains, on the whole, cells that are quite different from the cells of V2. The cells of V2 are, on the whole, different from the cells of V4 or V4a. If one were to judge globally, one would certainly be justified, at least based on the present evidence, in concluding that the analysis of different aspects of the visual environment may be emphasized in these different areas. However, the distinction is not all that clear cut. There are, for example, similarities in the color-coded cells of V4 and V4a. There are complex cells in V2 as well as in V4a. Although in the minority, there are color-coded cells in V2, and some of these have remarkable properties. By the same token, although also in the minority, there are non-color-coded cells in V4. It is not clear why there should be this duplication, if indeed it is a duplication. It is possible that these recurring cells may have different attributes in different areas and that we have simply not discovered them.

Convergent and Divergent Connections between Visual Cortical Areas

The existence of divergent connections from area 17 to the different prestriate areas—an obvious anatomical step for parceling out different types of information to different cortical areas—does not preclude the existence of convergent connections within each system. The anatomical evidence is that both strategies are simultaneously employed. An obvious example is the cortex of the posterior bank of the superior temporal sulcus. Although this zone receives one of the divergent outputs from area 17, the input to it from area
17 is highly convergent (Zeki 1971b). Moreover, the input to this visual cortical area from area 17 is convergent with the input to this same cortical field from V2. Thus after making a small electrolytic lesion in V2 and injecting tritiated leucine into area 17, one finds degenerating fibers and autoradiographic grains in the same part of the cortex of the posterior bank of the superior temporal sulcus (Fig. 12). Thus one may speculate, for example, that the properties of most of the cells of the superior temporal sulcus are built up by an input from area 17, and that the opposed movement complex cells, with the changing disparity that they are able to signal, are built up by an input from V2. This would be a logical and economical strategy for the cortex to use. Instead of sending multiple inputs to V2 for the analysis of fixed disparities and another set of inputs to the cortex of the posterior bank of the superior temporal sulcus for the analysis of changing disparities, one need only build up fixed disparity cells in V2 by a direct input from area 17 and then build up changing disparity cells in the cortex of the superior temporal sulcus by a direct input from V2. There is, of course, no evidence that this is necessarily the case; one could equally argue that all the properties of the cells of the superior temporal sulcus are built up by an input from area 17. The point is that the anatomical pathways are there, and it is not altogether implausible that such a strategy, or one similar to it, is used. Also, V4 receives an input from V2 and V3, in addition to the input from foveal 17 (although we do not know whether the two sets of inputs overlap), and it is possible that both the striate and prestriate inputs to V4 take part in building up the properties of the cells in this cortical field.

When one considers that there is a multiplicity of distinct anatomical areas within the visual cortex of the monkey (Zeki 1969, 1971a,b, 1972) and that each of these areas may have convergent inputs from one or from several antecedent areas and divergent outputs to more central cortical areas as well, then the possibilities for generating an endless variety of new cell types for analyzing in detail the many aspects of the visual environment become almost limitless.

Acknowledgment

This work was supported by the Science Research Council.
Figure 11. Reconstruction of a penetration through the cortex of area V4a of a rhesus monkey. To the left are shown the orientational preferences of the successive cells (dashed lines) and their preferred directions of motion (arrows). Numbers to the left of the column indicate the number of the cell; numbers to the right, the distances, in microns, between the cells. On the right in the figure is a tracing of a horizontal section to show the electrode track. The two small dots mark the positions of lesions made at the beginning and end of the track. All the cells in this penetration responded to the appropriate orientation regardless of wavelength. The dashed lines in the cortex indicate the limits of V4.

Figure 12. Tracings of horizontal sections through an experimental brain in which a small electrolytic lesion (black area in 1) was made in V2 and tritiated leucine was injected into area 17 (position marked by the four crosses in 2). The dots indicate the distribution of the degeneration following the lesion, and the crosses indicate the distribution of the autoradiographic grains following the injection of labeled leucine. Note that in the posterior bank of the superior temporal sulcus (3), the autoradiographic grains and the degeneration appear in the same region of the same section, showing that fibers from area 17 and from V2 converge on the same part of the cortex of the posterior bank of the superior temporal sulcus. LS, lunate sulcus; STS, superior temporal sulcus.
REFERENCES


———. 1971b. Convergent input from the striate cortex (area 17) to the cortex of the superior temporal sulcus in the rhesus monkey. Brain Res. 28:338.


