

UNIFORMITY AND DIVERSITY OF STRUCTURE AND FUNCTION IN RHESUS MONKEY PRESTRIATE VISUAL CORTEX

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SUMMARY

1. Recordings were made from single neurones, or small clusters of cells, in five prestriate visual areas of rhesus monkey cortex. The cells were studied for their binocularity, as well as for their orientational, motion and colour preferences. In all, 1500 cells were studied, 250 cells for each of the areas V2, V3, V3A and the motion area of the posterior bank of the superior temporal sulcus, and 500 cells for V4. All the cells referred to in this study can be placed in one prestriate area or another unambiguously.

2. The great majority of cells in all areas were binocularly driven, without monocular preferences. Within each area, there were cells that either preferred binocular stimulation markedly, or were responsive to binocular stimulation only. The ocular interaction histograms for all areas are remarkably similar when tested at a fixed disparity.

3. Over 70% of the cells in areas V2, V3 and V3A were selective for orientation. The receptive fields of cells were larger in V3 and V3A than in V2. By contrast, less than 50% of the cells in V4 and the motion area of the superior temporal sulcus were orientation selective.

4. Directionally selective cells were found in all areas. But they were present in small numbers (< 15%) in areas V2, V3, V3A and V4. By contrast, 90% of the cells in the motion area of the superior temporal sulcus were directionally selective.

5. 8% of the cells in V2 had opponent colour properties. Cells with such properties were not found in V3, V3A or in the motion area of the superior temporal sulcus. By contrast, 54% of the cells in the V4 complex had opponent colour properties.

6. It is argued that despite its uniformity in cytoarchitectural appearance and in ocular interaction patterns, there is a functional division of labour within the prestriate cortex. Evidence for this is seen not only in the different concentrations of functional cell types in distinct areas of the prestriate cortex, but also in the differential anatomical and callosal connexions of each area.

INTRODUCTION

Perhaps the single most striking feature of the visual cortex of the rhesus monkey is its size. Extending from the occipital lobe to the inferior temporal gyrus, and including the cortex buried within deep sulci, such as the calcarine, lunate and parieto-occipital, this visual cortex forms about one fifth of the entire neocortical surface in

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this species and much of it, beyond the striate cortex, is notable for its cytoarchitectural uniformity. One naturally asks why so much neocortex should be devoted to vision but curiosity is only partly informed by the demonstration of a multiplicity of areas within the prestriate visual cortex of this species, in each one of which the visual fields are separately represented, often in distinct ways, and each one of which has its own distinct ipsilateral and callosal connexions (see Zeki, 1974*a*, 1975 for reviews). Such evidence gives a powerful hint that different parts of the prestriate cortex must be specialized in ways that cytoarchitectural methods are ill suited to reveal, but raise, the obvious question why there should be so many different visual areas.

One answer has come from studying the responses of single neurones in anatomically defined visual areas of the prestriate cortex. Such an approach has provided the most convincing evidence yet of functional specialization within the prestriate visual cortex. In this paper, I present the results obtained by recording from 1500 cells in five anatomically well defined areas of the prestriate cortex, concentrating on four characteristics only, namely, binocularity, orientation selectivity, motion (directional selectivity) and colour. The aim has been to show that, superimposed on a cytoarchitectural appearance that varies little from one prestriate region to another, and an ocular interaction pattern which is also invariant when tested at a fixed disparity, there are remarkable differences in the properties of cells in different prestriate visual areas.

METHODS

Recordings were made from single cells or small groups of cells in monkeys anaesthetized with sodium pentobarbitone and paralysed with Flaxedil following procedures already described (Zeki, 1974*b*). In this study, it was important to be able to refer cells to specific areas of the prestriate cortex unambiguously – a procedure that is difficult in a field of uniform cytoarchitecture where there is no sharp boundary, in Nissl stained sections, between one area and another. In most of the recordings, I therefore used my earlier approach (Zeki, 1975) of sectioning the splenium of the corpus callosum and using the resulting degeneration as the anatomical marker.

It was not always necessary to use this approach, however. It was not used in recordings from the lateral part of V2 (the part lying next to V1), where there is no doubt about which area one is recording from. Nor was it used for recordings from the exposed surface of the prelunate gyrus (the fourth visual complex). But it was used in recordings from the motion area of the superior temporal sulcus which, cytoarchitecturally, has an uncertain boundary with the lateral part of the same sulcus (Zeki, 1977*b*). It was also used in recording from both V3 and V3A, neither of which has a clear cytoarchitectural boundary (Zeki, 1975, 1978*b*; Van Essen & Zeki, 1978). There did not appear to be any noticeable differences in the response of cells in animals with a sectioned corpus callosum and animals with an intact one for the properties considered here (see also Zeki, 1977*b*, 1978*b*).

At the termination of the experiments the monkeys were perfused transcardially with normal saline followed by a 4% solution of paraformaldehyde. The brains were sectioned and stained for Nissl substance or for silver degeneration, according to techniques already described (Zeki, 1970).

Criteria used for cell classification

(1) *Ocular interaction histograms.* The overwhelming majority of cells in all the prestriate areas recorded from were binocularly driven. There were, however, cells that were driven either exclusively by one eye or dominated by one eye. As well, some cells were driven only when both eyes were simultaneously stimulated. In preparing ocular interaction histograms, cells were divided into six categories thus: cells driven by the ipsilateral (I) or the contralateral (C) eye only (two categories), cells driven by both eyes, but dominated by the ipsilateral (ID) or contralateral (CD) eye (two categories); cells driven equally well by both eyes (B) (one category) and cells

driven only when both eyes are stimulated simultaneously (BO). Category B includes cells, of which there have been many examples, that are driven equally well by either eye but whose response is powerfully summated by binocular stimulation. Cells were tested at one disparity only.

(2) *Orientation*. Cells were classified as orientation selective if, when tested with slits, bars and edges, they showed an orientation preference and did not respond to the orthogonal orientation. There are cells, especially in V3 and V3A (see Zeki, 1978b), which show orientation specificities when tested with slits of light but also respond briskly to spots. Since when appropriately tested, they showed orientational preferences, they are included as orientation selective cells. The orientation histograms do not reveal differences in the fineness of tuning of orientation selective cells. This property varies somewhat from one cell to another, some not responding at 10° from the optimal orientation, whereas others tolerate deviations of 30°, or even more, from the optimal orientation. Where a cell responded to slits of any orientation as well as to spots, it was classified as non-orientation selective. In the histograms, the non-orientation selective cell group includes cells, found both in V2 and V3, which were inhibited by light (Zeki, 1978b).

(3) *Colour*. In classifying cells according to their colour preferences three categories were used. In one category are included cells that responded to the appropriate stimulus, regardless of the wave-length of the stimulus. Such cells are classified as non-colour coded. Cells that were colour coded were put in another category (see Text-fig. 1). For a cell to be classified as colour coded, it had to meet the following requirements. It had to respond to one part of the spectrum only and not to other parts or to white light at the highest intensities available (for white light the highest intensity, reflected off the screen, was 150 lux). The absence of a response to white light indicated that, at some stage, such a cell must receive an opponent colour input, even though the opponent mechanism was not always elicitable (Zeki, 1977b). Cells having the above characteristics were therefore classified as OPPONENT COLOUR cells. As with the orientation histograms, the colour histograms do not indicate how finely these cells are tuned for colour. As I have indicated elsewhere (Zeki, 1977b), the range of the spectrum that colour coded cells respond to varies from one cell to another, but these ranges are not given here. In a third category are included cells which responded to all parts of the spectrum, as well as to white light, but greatly preferred one colour over another. A cell might, for example, respond much better to the red end of the spectrum than to blue or green or white light. When the response to one colour, as judged by ear, was markedly better than the response to other colours or to white light, but where there was no evidence of an opponent colour mechanism, the cell was classified as COLOUR BIASED. Action spectra for a non-colour coded cell, a colour coded cell and a colour biased one are given in Text-fig. 1. A careful inspection of this Figure will show that it is sometimes difficult to distinguish between a colour biased and a non-colour coded cell.

(4) *Motion*. For a cell to be classified as directionally selective, it had to respond to motion in one direction and not to respond at all to motion in the opposite direction. As with orientation and colour, the fineness of directional tuning is not indicated in this category. Where a cell responded to motion in two opposite directions but markedly preferred one over another, it was classified as a directionally biased cell.

(5) *Numbers of cells*. For areas V2, V3 and V3A and the movement area of the posterior bank of the superior temporal sulcus, the statistics of 250 cells for each area are given. For the fourth visual complex (V4), however, statistics are given for 500 cells. More cells were sampled from the V4 complex because of its immense anatomical complexity (Zeki, 1971, 1977a; Van Essen & Zeki, 1978).

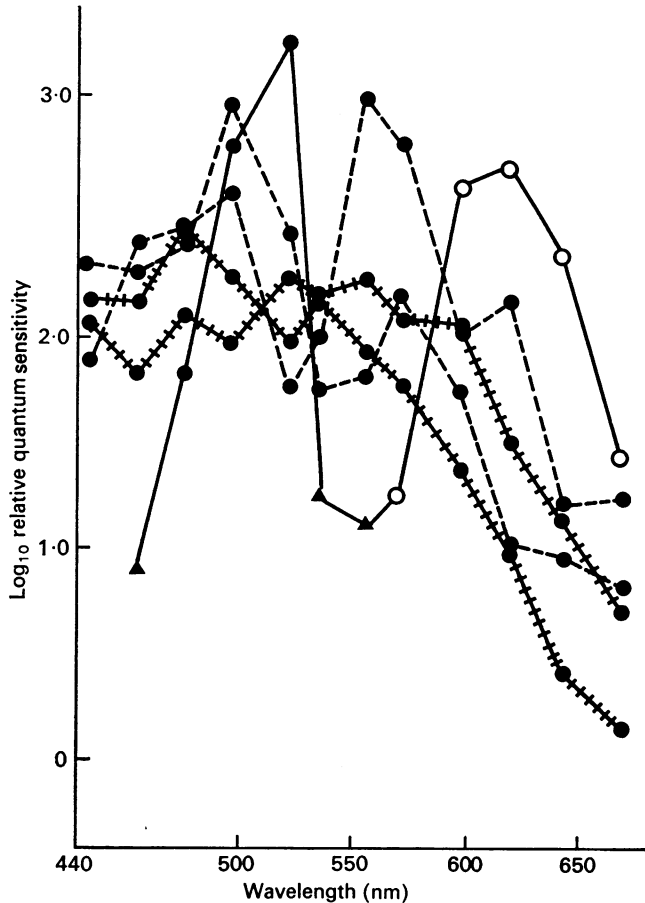
For all areas, only the first 250 cells (or 500 in the case of V4) about whose location there was no doubt are included in the statistics. The total, 1500, does not represent the total number of cells recorded from.

RESULTS

I. *Uniformity of cytoarchitecture and of ocular interaction patterns in five prestriate areas*

Pl. 1 shows two low power photo-micrographs of horizontal sections through the lunate and parieto-occipital sulci of a rhesus monkey whose callosal splenium had been sectioned 6 days before sacrifice. The brain sections were stained for silver

degeneration and counter-stained for Nissl substance. Pl. 1A is taken in bright field illumination to show the cytoarchitecture of this part of the prestriate cortex and Pl. 1B is a dark field photomicrograph of the very same section, to show the degenerating callosal fibres. The remarkable cytoarchitectural uniformity of the

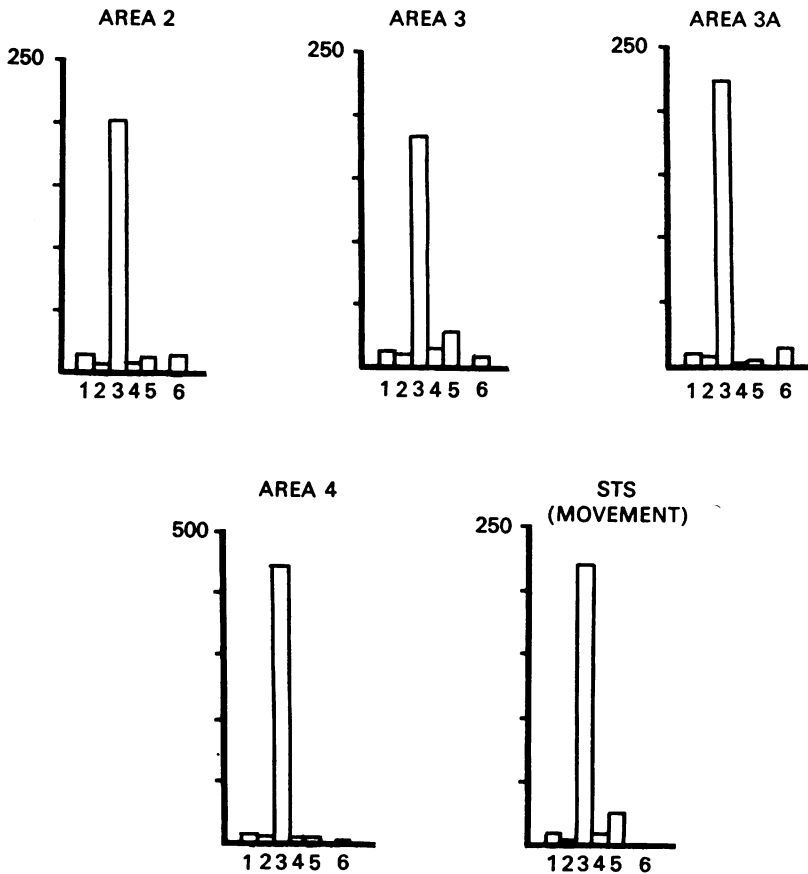


Text-fig. 1. Action spectra for non-colour coded, colour biased and opponent colour cells, as defined in the text. The action spectra for non-colour coded cells were from cells in the motion area of the superior temporal sulcus and from V3. The colour biased cells were from V3 and V4. The opponent-colour cell was from V4. Filled circles on responses; open circles, OFF responses; triangles, NO response at the highest intensities available. —, colour opponent cell; ----, colour biased cell; + + +, broad band cell (non-colour coded).

prestriate cortex as one proceeds from one area to another is obvious, any differences in the thickness of the laminae being almost certainly due to fissuration and obliquity of sectioning, since these differences do not respect areal boundaries. That this is so is evident at a glance by comparing Pl. 1A with Pl. 1B. The latter shows the areas of callosal degeneration which can be used to advantage in drawing the boundaries of the prestriate areas (Zeki, 1975, 1978b; Zeki & Sandeman, 1976; Van Essen & Zeki, 1978). When these boundaries are drawn (1C), it becomes obvious that there is no

cytoarchitectural criterion which helps in distinguishing one prestriate area from another.

The power of the two eyes to drive single cells in these different prestriate areas is also remarkably uniform. Text-fig. 2 gives ocular interaction histograms for the five prestriate areas. Without the label, it would be difficult to tell one area from another and, indeed, if all the data were to be pooled into one histogram, the shape would be similar to the individual histograms of Text-fig. 2. Not all the information available



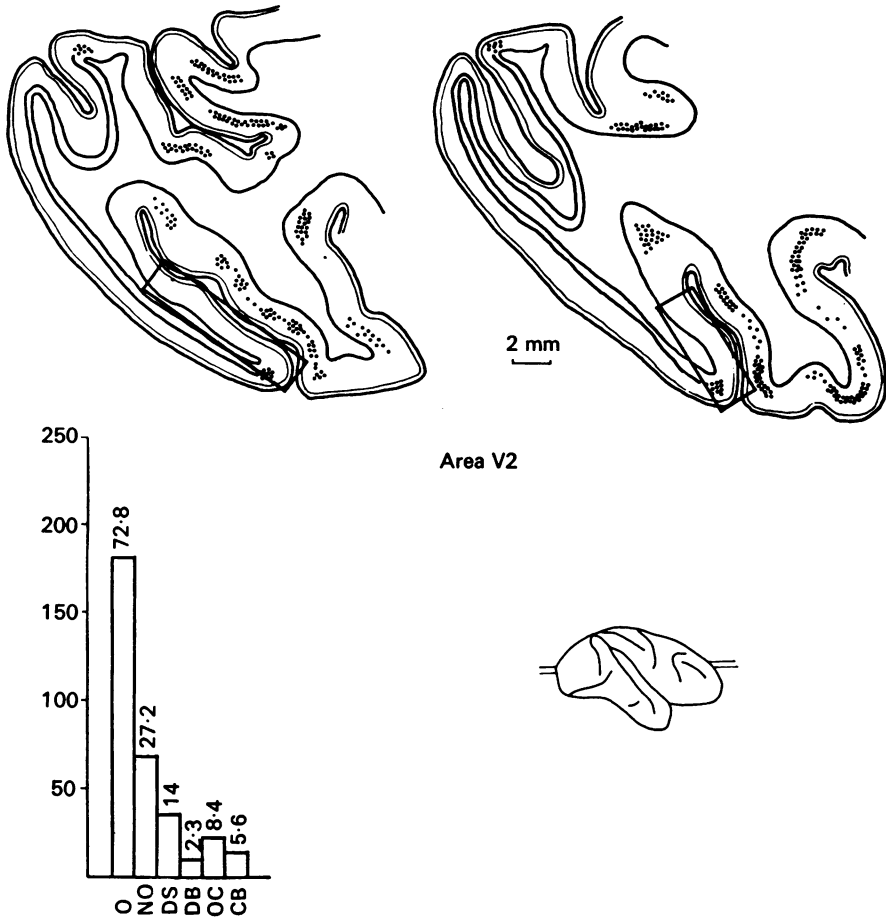
Text-fig. 2. Ocular interaction histograms for the five prestriate areas studied in this paper. The histogram for each area, except V4, is based on 250 cells. For V4, the histogram is based on 500 cells. 1, cells driven by the ipsilateral eye only. 2, cells dominated by the ipsilateral eye. 3, binocularly driven cells. 4, cells dominated by the contralateral eye. 5, cells driven by the contralateral eye only. 6, cells activated by binocular stimulation only. Category 6 cells also occur in the movement area but were not found in the first 250 cells used in these statistics.

on ocular interaction patterns is given in these histograms. For example, in area V2, I have encountered cells which are unresponsive when both eyes are stimulated but give a good response to stimulation of an individual eye. These did not occur among the first 250 cells entered in the statistics but such examples have been very rare and

their inclusion would not in any way modify the essential similarity of the ocular interaction patterns in the five prestriate areas, as tested at a fixed disparity.

II. *Functional heterogeneity in five prestriate areas*

Despite this uniformity of cytoarchitecture, and of ocular interaction patterns, the prestriate cortex is not a uniform area. Although this is implicit in the differential connexions of its different parts, it is most clearly shown by differences in the



Text-fig. 3. To the lower left is a histogram showing the proportions of cells in area V2 responsive to the different categories of specific visual stimuli considered in this paper. Above are tracings of two horizontal sections, taken at the levels indicated on the surface drawing of the brain to the right. The dots in the cortex represent the regions of callosal fibre degeneration in the prestriate cortex following transection of the corpus callosum. The boxed areas represent regions of the cortex which were accepted as being in area V2. These regions would be acceptable as being in V2 even in the absence of additional anatomical landmarks such as provided by the callosal fibre degeneration (see Zeki, 1969a). It is to be noted that the regions of V2 recorded from in this study represent the central 5° of the visual fields only. Continuous line in the cortex represents area 17 (V1). LS, lunate sulcus. O, orientation selective cells. NO, non-orientation selective cells. DS, directionally selective cells. DB, directionally biased cells. OC, opponent-colour cells. CB, colour biased cells. The figure above each column in the histogram gives the percentage.

physiological properties of cells as one surveys different, anatomically well defined, areas of the prestriate cortex.

(A) *The second visual area (V2)*

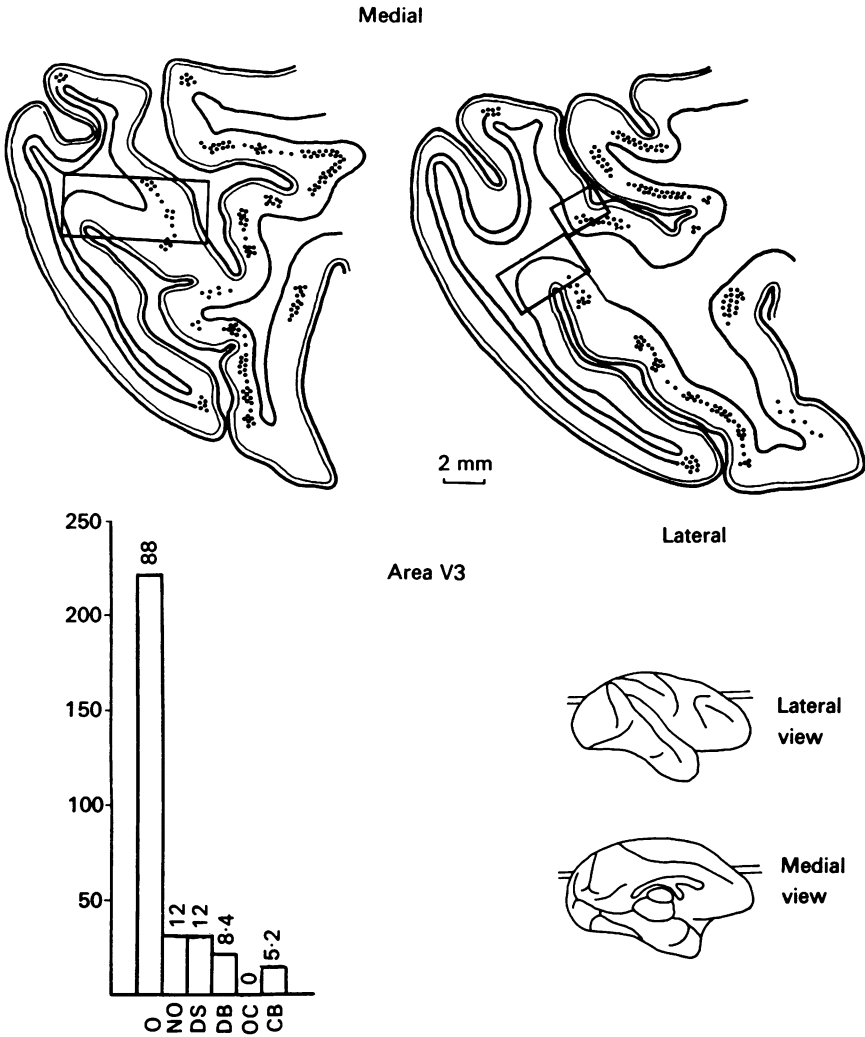
The second visual area surrounds the striate cortex (V1) and receives a direct, topographically organized, input from it (Cragg, 1969; Zeki, 1969*a*). Where recordings were made from V2 in the lunate sulcus, special anatomical markers are not necessary to make certain that the recordings were from V2, especially if these are made in the lateral part of V2, in the posterior bank of the lunate sulcus. This is not the case for the lower part of V2 (representing the upper visual fields) which lies in the inferior occipital sulcus. Because of the complex relationship of the lower part of V2 with V4 (Zeki, 1970, 1971), special anatomical markers are necessary. In the present study, all the recordings in V2 were made in the posterior bank of the lunate sulcus. The regions from which recordings were made and which are acceptable, without any doubt or ambiguity even in the absence of callosal landmarks, as being in V2 are boxed in the sections shown in Text-fig. 3.

Perhaps the most striking feature of V2 is the heavy concentration of orientation selective cells (about 75%), even though cells not selective for orientation are also present (see Text-fig. 3). Other functional categories are also represented in V2. For example, 14% of the cells in this area had clear directional selectivities and 2.3% were directionally biased. The percentage of opponent-colour cells was low (8.4%) and 5.6% of the cells were colour biased. Hence the total percentage of cells in V2 showing colour selectivity in their responses is 14%, a figure not much higher than that given for area 17 (V1) by Hubel & Wiesel (1968). In considering the colour selectivities of cells in V2, it is important to emphasize that the receptive fields of all the cells recorded from in this area were within the central 5°, a region in which colour vision is good.

In summary, then, although representatives of all types of cells are found in V2, the highest concentration is of orientation selective cells.

(B) *The third visual complex*

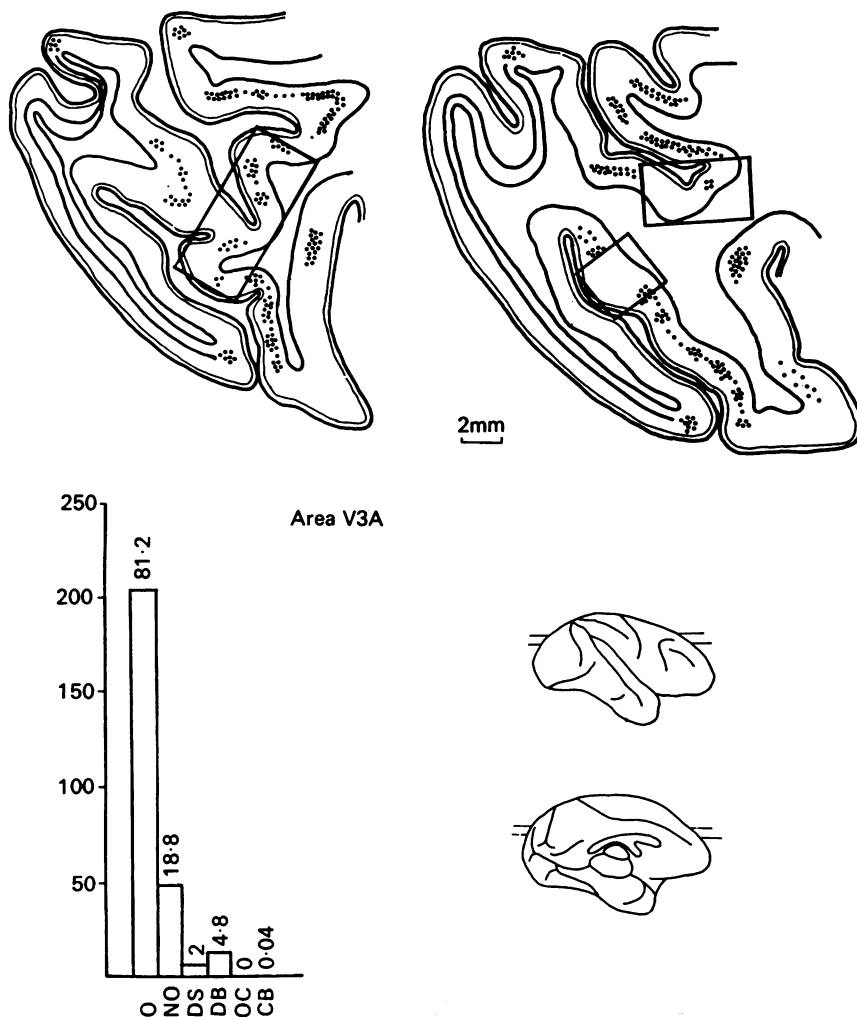
(i) *Area V3*. Area V3, like V2, receives a direct input from V1 (Cragg, 1969; Zeki, 1969*a*, 1977*a*), although the anatomical characteristics of this input are different to those of V2 (Zeki, 1978*b*). To be certain that one is recording from V3 is difficult in the absence of additional anatomical landmarks (Zeki, 1975, 1978*b*). The horizontal meridian forms a common boundary between V2 and V3 (Cragg, 1969; Zeki, 1969*a*, 1977*a*), but there is no cytoarchitectural landmark to indicate where this boundary may be. Anteriorly, the boundary of V3 with V3A, an area not receiving a direct input from V1 (Zeki, 1978*b*), is also cytoarchitecturally uncertain (Van Essen & Zeki, 1978). Consequently, the statistics given below include only cells which were unambiguously located in V3 through the use of callosal degeneration landmarks. The regions of the prestriate cortex which were accepted as being unambiguously V3, in the presence of callosal degeneration landmarks, are boxed in Text-fig. 4. Evidence is presented elsewhere (Zeki, 1977*b*, 1978*b*) to show that sectioning the splenium of the corpus callosum does not disrupt, in any obvious way, the properties of the cells in these prestriate areas, at least not the ones considered in this paper.



Text-fig. 4. To the lower left is shown the distribution of the different categories of cells in V3. Above are tracings of horizontal sections, taken at levels indicated on the surface drawings of the brain to the right, to show the regions of the prestriate cortex which are acceptable as being V3, on the medial (parieto-occipital sulcus) and lateral (lunate sulcus) sides. Conventions as in Text-fig. 3. Although V3 has an uncertain cytoarchitectural boundary with V2 posteriorly, anatomical experiments (Zeki, 1977b) show that the depth of the lunate sulcus at the levels indicated here is occupied by V3. Consequently no special anatomical landmarks are needed if recordings are made from the depth of the lunate sulcus at the levels shown here. The boundary of V2 with V3 in the parieto-occipital sulcus is uncertain and only recordings in the region of the first patch of degeneration after the V1-V2 boundary were accepted as being in V3. There is no cytoarchitectonic boundary between V3 and V3A, lying more anteriorly. Consequently the technique of sectioning the callosum before recording was used and only cells which fell within the medial end of the first patch of callosal degeneration after the V1-V2 boundary were accepted as being in V3. CS, calcarine sulcus; POS, parieto-occipital sulcus.

The statistics for the 250 cells in V3 are shown in Text-fig. 4. Even more striking than in V2 is the heavy concentration of orientation selective cells in this area (88% of the total number studied). Just as in V2, other functional categories are also represented in V3 but, once again, the proportions were low, 12% of the cells being directionally selective and 8.4% directionally biased. No opponent-colour cells were found in V3, but 5.2% of the cells showed some degree of colour bias.

(ii) *Area V3A*. The histogram for V3A shows such a striking similarity to that of



Text-fig. 5. Histogram of the percentage distribution of cells in area V3A. Conventions as in previous Figures. Since V3A has a cytoarchitecturally uncertain boundary with V3 posteriorly and V4 anteriorly, additional anatomical landmarks to make certain one is recording from V3A are mandatory. Consequently, all the cells used in the statistics for V3A were derived from brains in which the splenium of the corpus callosum had been sectioned before the recording experiments. The regions of the prestriate cortex acceptable as being in V3A, at the levels indicated, are boxed in the tracings of the horizontal sections shown above. For further details, see text (and also Zeki, 1977b; Van Essen & Zeki, 1978).

V3 that it would be impossible to tell, in the absence of a detailed knowledge of where the recordings were made from, which subdivision of the third visual complex each histogram belongs to. This forms perhaps the most powerful reason for grouping the two areas together, even though they are two different areas, in each one of which the visual fields are separately represented and which differ in their anatomical inputs and topographic organization (Van Essen & Zeki, 1978; Zeki, 1978*b*). The boundaries of V3A with V3 and V4 are extremely difficult, if not impossible, to determine cyto-architecturally (Van Essen & Zeki, 1978; Zeki, 1978*b*). Consequently, all the recordings from V3A included here are from animals in which the degeneration produced by sectioning the splenium of the corpus callosum made it possible to be certain that the recordings were indeed from V3A. As before, regions of the cortex which were accepted as being V3A in the presence of such landmarks are boxed in the summary Figure for V3A (Text-fig. 5).

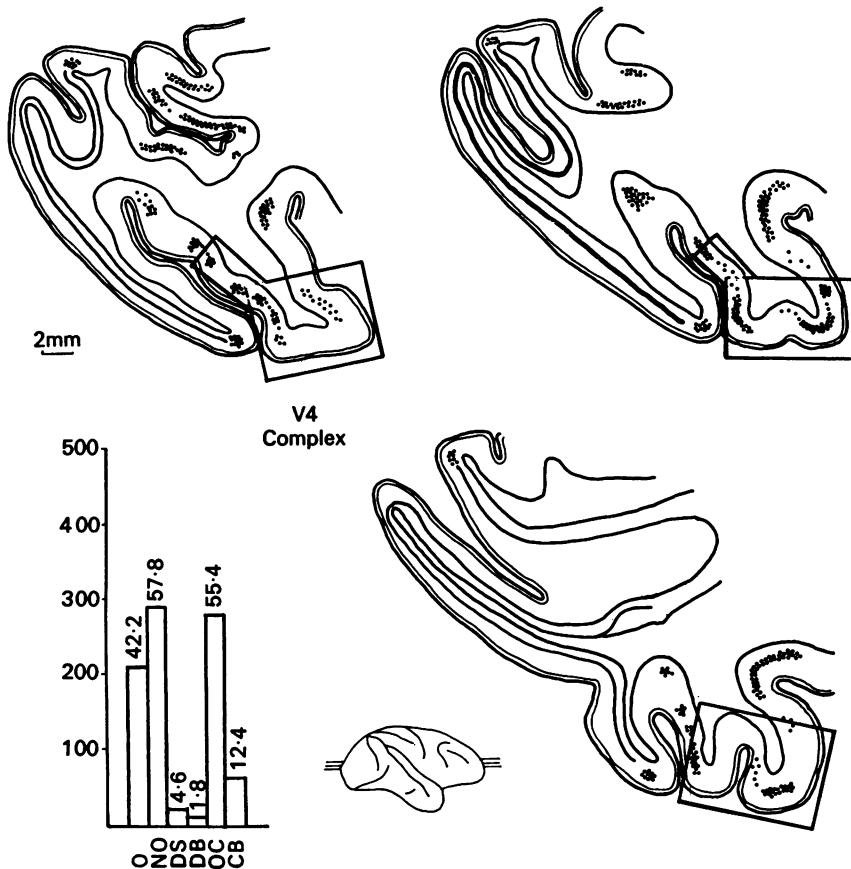
As with area V3, there is a heavy concentration of orientation selective cells and relatively few of the other types of cells considered in this study. 2% of cells were directionally selective cells, and 4.8% showed a directional bias. Like V3, there were no opponent-colour cells and only 1 cell (0.04%) showed a colour bias.

It is quite clear from the results shown in Text-fig. 2 that both areas V3 and V3A contain cells which are responsive only when both eyes are simultaneously stimulated. These cells may well be of importance in analysing binocular disparity. The recordings made by Hubel & Wiesel (1970) in the annectant gyrus also yielded many such cells. Since the annectant gyrus is occupied partly by V2, partly by V3 and partly by V3A, it is probable that their recordings involved all three areas. I have not studied such cells in any detail and, consequently, it is not possible to tell from this study whether there are any differences in the proportions, or the quality, of these cells in these three areas.

(iii) *The fourth visual complex (V4)*. Lying lateral to area V3A in the anterior bank of the lunate sulcus, and extending on to the prelunate gyrus, are the fourth visual areas. This part of the prestriate cortex contains heavy concentrations of colour coded cells (Zeki, 1973, 1975). There is another region of the prestriate cortex which contains large numbers of colour coded cells and this lies laterally in the posterior bank of the superior temporal sulcus. Because of the striking functional similarities of cells in this entire region, I have argued elsewhere (Zeki, 1977*b*) for including the entire region in one area (the fourth visual complex) within which there are two or more subdivisions. Certainly, despite differences in anatomical input (Zeki, 1971, 1977*b*, 1978*a*), it is remarkably difficult to tell whether one is recording from the lateral part of the anterior bank of the lunate sulcus or from the lateral part of the posterior bank of the superior temporal sulcus until the histology is available. In the statistics given below, therefore, the entire region is considered as a single zone.

Although there is no doubt that one would be recording from the fourth visual complex if the electrode were to sample from cells in the cortex of the prelunate gyrus below the level at which the annectant gyrus disappears, it becomes much more difficult to be certain of the exact locus when recordings are made in the anterior bank of the lunate sulcus where V4 has a common boundary with V3A (Van Essen & Zeki, 1978) or in the posterior bank of the superior temporal sulcus where this zone may have a common boundary with the motion area which lies more medially within

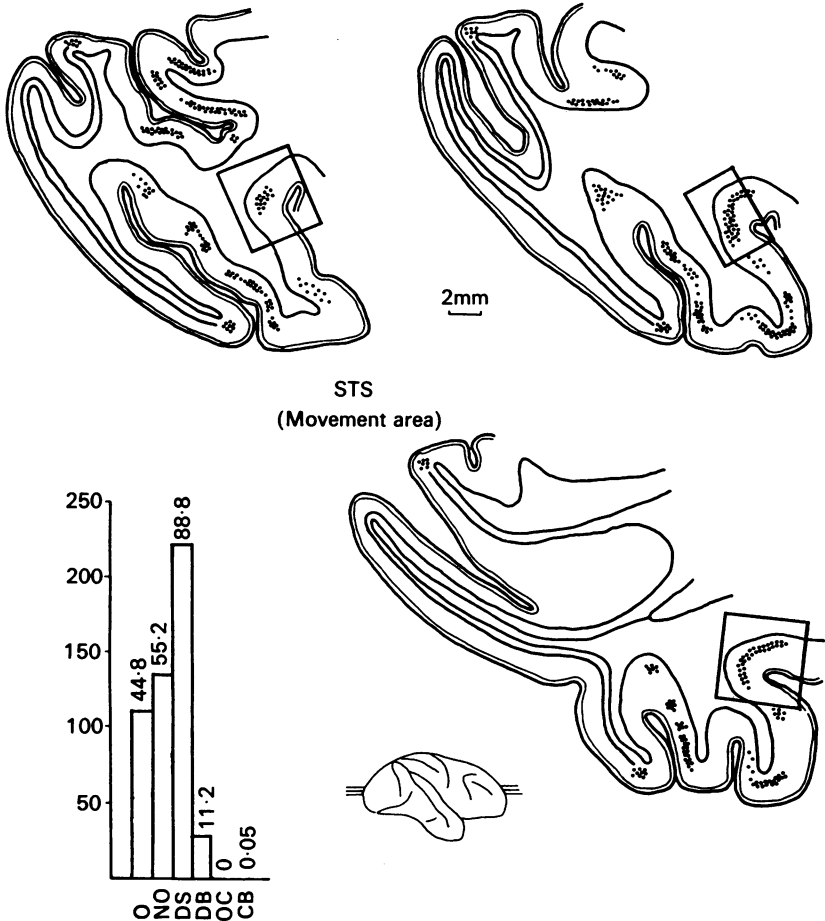
the same sulcus (Zeki, 1977b). Consequently, in this study, cells situated in the cortex of the prelunate gyrus were accepted as belonging to V4, even where no special anatomical landmarks were available, such as the degeneration produced by sectioning the corpus callosum. On the other hand, where the recordings were made from those parts of the V4 complex which lie in the anterior bank of the lunate sulcus or



Text-fig. 6. Histogram of the percentage distribution of cells in V4. For the purposes of the present paper, V4 is considered to extend from the anterior bank of the lunate sulcus to the lateral part of the posterior bank of the superior temporal sulcus (see Zeki, 1978b). Recordings made on the surface of the prelunate gyrus, at the levels indicated in this figure, are acceptable as being in V4 even in the absence of additional anatomical landmarks. However, where recordings are made from V4, in the anterior bank of the lunate sulcus or in the posterior bank of the superior temporal sulcus, additional anatomical landmarks are necessary (see text). For the purposes of this study, the recordings from these parts of V4 were made in animals in which the splenium of the corpus callosum had been sectioned. The resulting fibre degeneration allowed a more definite boundary to be drawn between V4 and its surrounding areas. Regions acceptable as being V4 are boxed in the section drawings. Conventions as in previous figures.

the posterior bank of the superior temporal sulcus, they were acceptable as having been in V4 only if additional anatomical landmarks were available. The regions of the prestriate cortex which were accepted as being V4, and from which recordings were

made, are boxed in Text-fig. 6. The histogram distribution of the V4 complex, also shown in Text-fig. 6, shows a remarkable difference to those of V2, V3 and V3A. Unlike these three areas, there is a fall in the percentage of orientation selective cells to below 50% and, by contrast, the percentage of cells not showing orientational selectivity rises to 57.8% (from 27.2% in V2, 12% in V3 and 18.8% in V3A).

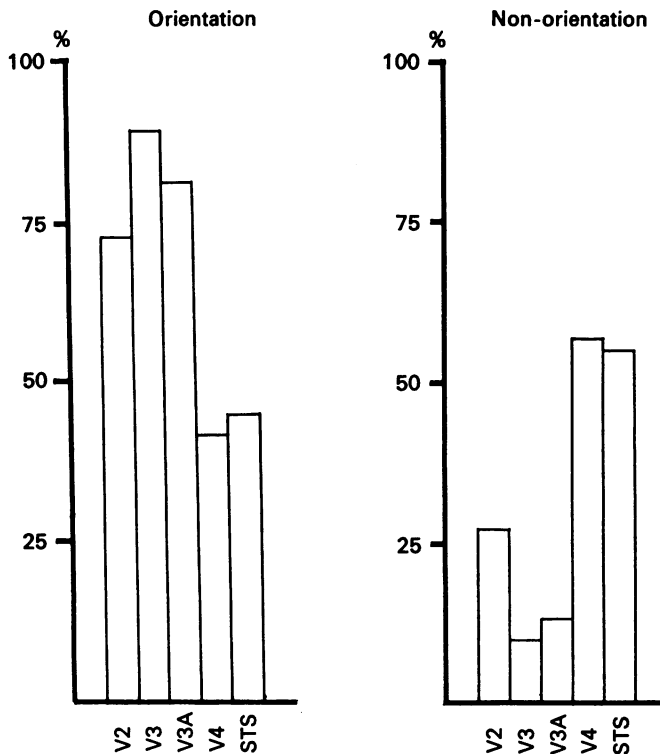


Text-fig. 7. Histogram of the percentage distribution of cells in the movement area of the superior temporal sulcus. This area has a cytoarchitecturally uncertain boundary with the more lateral region of STS which may be part of V4 but the distribution of callosal fibres helps to resolve this boundary (see Zeki, 1978b). Regions of the superior temporal sulcus acceptable as being part of the movement area are boxed in the section drawings. Conventions as in previous Figures.

Directionally selective cells and directionally biased ones are small in number (4.6 and 1.8% respectively). By contrast there is a large increase in the number of colour coded cells which, in V4, form 55.4% of the population, and also in the number of colour biased cells which form 12.4% of the population.

(iv) *The motion area in the posterior bank of the superior temporal sulcus.* This area lies more medially in the posterior bank of the superior temporal sulcus. In this study,

cells were accepted as being in the motion area if the recordings were in the very medial part of the sulcus, even in the absence of additional anatomical landmarks. However, where the recordings were from more lateral parts of the sulcus, they were only accepted as having been made in the cortex of the motion area if additional anatomical landmarks such as the degeneration produced by sectioning the corpus callosum were available. This is because as stated earlier, the motion area has a cytoarchitecturally uncertain boundary with the lateral part of this sulcus, which, in this paper, is grouped in the fourth visual complex.



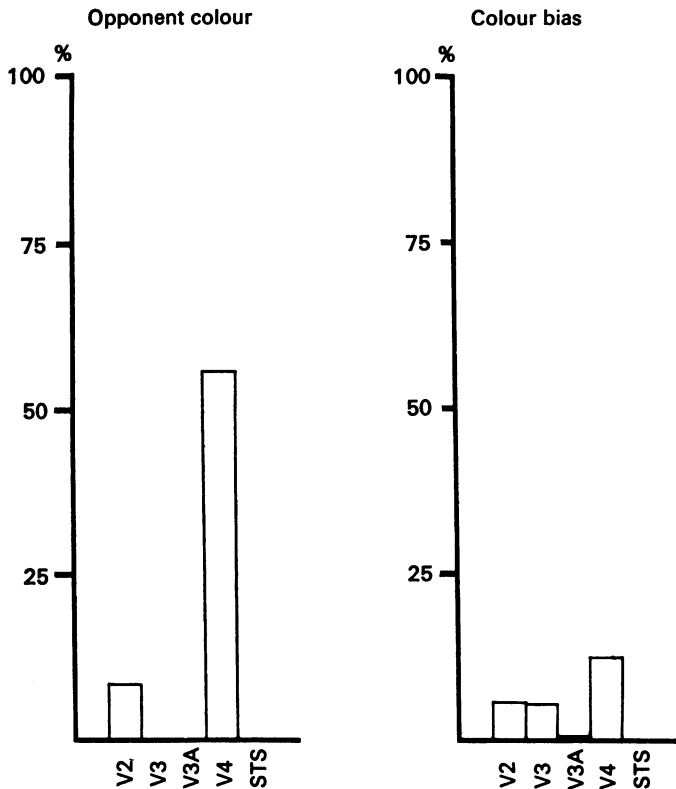
Text-fig. 8. The percentage distribution of orientation selective cells in five prestriate areas.

Text-fig. 7 shows the histogram for 250 cells in the motion area of the posterior bank of the superior temporal sulcus. The proportions of orientation selective cells is similar to that of V4, but markedly lower than those of V2, V3 and V3A. The percentages of colour opponent cells (0%) and colour biased ones (0.05%) is similar to what is found in V3 and V3A, but lower than for V2 and V4. By contrast, confirming earlier results (Zeki, 1974*b*), the percentage of directionally selective cells soars to 88.8%. This area, therefore, stands in marked contrast to the previous areas in the heavy concentrations of directionally selective cells to be found here.

The analysis of orientation, motion and colour in the prestriate cortex

Although the detailed histograms given above show that there are substantial differences in the proportions of the different types of cells contained in the five

prestriate areas, an alternative, and perhaps more convincing, way of displaying these differences is to consider any one type of property, for example orientational selectivity, and to plot the percentage distribution of cells exhibiting that property against the five prestriate areas in a single histogram. This is done for orientational selectivity, colour opponency and directional selectivity in Text-figs. 8, 9 and 10. In Text-fig. 8, the percentage distribution of orientation selective cells in the different prestriate areas is shown. It is obvious that the highest concentration of orientation selective cells occurs in V2, V3 and V3A, whereas in V4 and the motion area of the

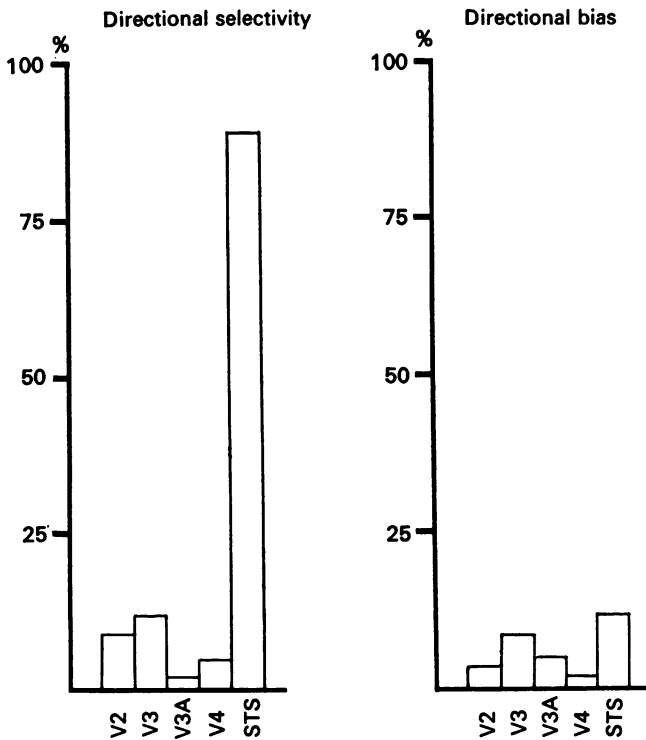


Text-fig. 9. The percentage distribution of colour opponent and colour biased cells in five prestriate areas.

superior temporal sulcus, the percentage of cells showing orientational selectivity falls to below 50%. It might appear from such a histogram that areas V2, V3, and V3A should be grouped together. But this need not be the case. For example, if one were to plot receptive field sizes in V2, V3 and V3A, it would be easy enough to distinguish V2 from V3 and V3A, the sizes in the former being smaller than the latter two (S. M. Zeki, unpublished results). The distinction between V3 and V3A, on the other hand, is a little more difficult to make on this basis. Despite differences in their anatomical inputs, geographical locations, and topographic organization, and despite the separate representation of the visual fields in each area, these two areas have remarkably similar populations of cell types as studied by these rather crude methods.

More sophisticated analyses will probably be required to distinguish between them functionally.

When one turns to the colour histogram (Text-fig. 9) one is struck by the heavy concentration of colour-opponent cells in V4, the low concentration of such cells in V2 (even in regions of V2 representing the central 5° of the visual fields from which the recordings reported here were made), and the absence of colour opponency in V3, V3A and the motion area of the superior temporal sulcus. The conclusion seems, inescapable that there is a heavy concentration of opponent colour cells in the fourth visual complex compared to other prestriate areas, in harmony with results reported earlier (Zeki, 1973, 1975, 1977*b*).



Text-fig. 10. The percentage distribution of directionally selective cells in five prestriate areas.

Finally, when one turns to the histogram (Text-fig. 10) for directional selectivity, it is obvious at a glance that, although all of the areas reported here have directionally selective cells, the heaviest concentration occurs in the motion area of the superior temporal sulcus. It is for this reason that the argument has been made (Zeki, 1974*b*) that this area is especially concerned with analysing motion in the visual fields.

DISCUSSION

That the prestriate cortex of the monkey has a uniform cytoarchitectural appearance has been well known for over seventy years. In one of the earliest papers on the cytoarchitecture of the prestriate cortex in the monkey, Campbell (1905) experienced

great difficulties in demarcating it because '...the general transitional changes which the area undergoes at its borders are gradual instead of abrupt; especially is this the case where the field joins the temporal and parietal areas'. Brodmann, writing at the same time (1905), made of his cytoarchitectonic area 18 a large cortical field which, on the lateral side, would include areas V2, V3, V3A and V4 but possibly not the motion area of the superior temporal sulcus much of which falls within Brodmann's cytoarchitectonic area 19. Even this modest subdivision was not acceptable to other workers in the field (see Zeki, 1969*b* for review). Indeed Lashley & Clarke (1946) claimed that 'areas 18 and 19 (of Brodmann) are indistinguishable from each other and from area 7 and probably form a functional unit with the latter'.

Yet a single 'functional unit' is precisely what the prestriate cortex is not. This has been implicit since 1969 when it was shown that different parts of this cytoarchitectonically uniform prestriate cortex receive different, and independent, inputs from area 17 (Cragg, 1969; Zeki, 1969*a*), and have independent callosal connexions (Zeki, 1970). Since that time the anatomical autonomy of other prestriate areas has been shown (Zeki, 1971, 1977*b*, 1978*b*) so that, anatomically at least, the cytoarchitecturally uniform prestriate cortex can be subdivided into a set of independent areas.

It would be astonishing if there were no functional differences between these areas to reflect these anatomical differences. Recordings from single cells in these different prestriate areas, summarized in this paper, show that there are, indeed, heavy concentrations of different cell types in these distinct anatomical areas. The criteria that I have used are, of course, limited and by the use of further criteria it is likely to be possible to further distinguish one area from another. For example, V2 and V3 can be distinguished from each other by the receptive field sizes of the cells in the two areas. It would be interesting to know whether there are any differences in the types of binocular disparity cells contained in V2, V3 and V3A. In this context it is worth recalling that cells which, though equally well driven by either eye, summate their response to binocular stimulation may also be detectors of binocular disparity. Again, in spite of V3 and V3A being separate areas (since the visual fields are separately represented in each area, and since they differ from each other in anatomical input, callosal connexions and topographical organization), it has still not been possible to distinguish between them functionally in a convincing way. To do so would probably require a study of many more cells and a more detailed analysis of other properties, such as, for example, fineness of orientational tuning. Equally, I have not been able to distinguish between the various subdivisions of the fourth visual complex of areas where marked functional differences between one region and another are yet to be found (see Zeki, 1977*b*).

Despite these difficulties, however, single cell recordings from anatomically well defined parts of the prestriate cortex amply confirm what one suspected since 1969, namely that the cytoarchitectonically drab and monotonous prestriate cortex is, after all, a highly differentiated field of cortex. And this very differentiation, into areas, each of which may be specialized to analyse a different aspect of the information contained in the visual environment, is one clue to the extensive size of the visual cortex in the rhesus monkey. Instead of analysing all the visual information in one area or region, the cortex does so in separate areas, emphasizing some functions in

one area, other functions in another. It is almost certain that each one of the areas discussed here has other functions, besides what has already been found. It is also possible that there are further uniformities between these areas, beyond what has been described. For example, isolated examples of cells with a high maintained discharge, which are inhibited by light, have been found in V2 and V3, as well as V1 (Zeki, 1978*b* and unpublished results). This clearly is a category of cell represented in all three areas. What further uniformities exist between these areas, the functional significance of these uniformities, what further functions each area has, and how the information analysed in these areas is assembled at even more central visual areas remains one of the most challenging of problems in visual neurophysiology.

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EXPLANATION OF PLATE

A and *B* are low-power photomicrographs of a small region of a horizontal section taken through the lunate and parieto-occipital sulci of a monkey whose corpus callosum had been sectioned. The region of the section shown in the photomicrographs is boxed in the drawing of the horizontal section from which these photographs were taken. The dots in the cortex represent degenerating callosal fibres. The section was stained for fibre degeneration and counterstained for Nissl substance. In *A*, the cytoarchitectonic picture of this part of the prestriate cortex, as revealed in a Nissl-stained section, photographed in bright field, is shown. *B* is a photomicrograph of the same section, but taken in dark field, to show the degenerating callosal fibres (seen as white in the cortex). Based on the distribution of the callosal fibres, three different areas in this part of the prestriate cortex are recognizable, and these are entered in the drawing of the section. It is evident, by comparing *A* and *B*, with *C*, that the borders of these areas do not fall in regions with recognizable cytoarchitectonic differences.



5 mm

