

# review article

## Functional specialisation in the visual cortex of the rhesus monkey

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*Anatomical and functional studies of the visual cortex of the rhesus monkey have shown that it is made up of a multiplicity of distinct areas. These seem to be functionally specialised to analyse different features of the visual environment.*

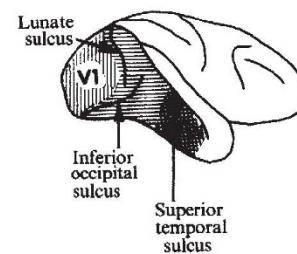
THE cerebral cortex is the largest and most impressive part of the nervous system, in both monkey and man. There are several features that distinguish it from other parts of the nervous system. Perhaps chief of these is the enormous number of nerve cells that it contains<sup>1</sup>. How this mass of nervous tissue is organised has been a subject of very considerable interest. For a long time, clinical neurologists believed that different functions, such as vision, audition, language, memory for words, memory for colours, and so on, were localised in structurally distinct regions of the cerebral cortex. The evidence for this was based partly on clinical studies from which it is rarely possible to know the exact location and size of the pathological changes in the cortex. It was also based in part on the anatomical method of cytoarchitectonics, which analyses how cells in different parts of the cerebral cortex are grouped into layers. Differences in the layering pattern of cells between different cortical regions were thought to reflect functional differences. This is undeniably so for some parts of the cortex. The structure of the motor cortex, to take one of the best known examples, is so different from that of the immediately adjoining sensory cortex, that it would be hard to imagine that this does not reflect the well known functional differences between the two areas. But such clear examples are the exception rather than the rule. Even determined students of cytoarchitectonics conceded that extensive regions of the cortex are of uniform cytoarchitecture<sup>2,3</sup>. Of the remaining differences that they described, many were almost certainly the secondary consequence of the fissuration and foldings of the brain<sup>4</sup>.

Theories of functional localisation were, therefore, greatly compromised by technical difficulties and uncertain methods: hence they came to be questioned<sup>5</sup>. But they were not replaced by an alternative theory, based on more certain techniques. The problem itself thus remains, and is worth investigating with new methods. It can be made more manageable by restriction to a single system, such as the visual system, especially in an animal with a highly developed visual capacity, such as the rhesus monkey. One can then ask: how is the visual cortex organised to handle all the information available to it?

Considered cytoarchitecturally, the entire visual cortex of the rhesus monkey can be subdivided into two major zones (Fig. 1). Posteriorly, the striate cortex is so distinct and uniform that its borders are visible, in histological sections, even to the naked eye. The visual hemifields are completely mapped in the striate cortex<sup>6,7</sup>. Most of its cells are responsive to contours of

specific orientation<sup>8</sup> and although they tend to respond better to stimulation of one eye or the other, most of them can be influenced by stimulating either eye<sup>8</sup>. Two of the functions of the striate cortex, therefore, are the bringing of the inputs from the two eyes together and the detailed analysis of the visual fields for contour. Anterior to the striate cortex, and surrounding it, is another uniform field, of different cytoarchitectural design, known as the prestriate cortex (Fig. 1). Although the prestriate cortex has a very sharp boundary with the striate cortex, its anterior limits are very uncertain. Even its boundary with the inferior temporal cortex, a geographically separate area, but one well known from behavioural studies to be visual in function<sup>9,10</sup> is uncertain. Because no clear cytoarchitectonic differences are evident over large extents of the prestriate cortex, much of it (for example Brodmann's area 18)<sup>3</sup> was considered, mistakenly as we now know, to be a single cortical 'area'. Others proposed to include even further cortical regions in this single area<sup>9</sup>.

The only part of this entire visual cortex that receives a direct input from the eyes, through the lateral geniculate nucleus, is the striate cortex<sup>11</sup>. Because of this arrangement of the visual projections, in monkey as well as in man, the striate cortex was referred to as the 'visuo-sensory' cortex<sup>2</sup>. The prestriate cortex, not receiving a direct projection from the eye, was presumed to be the site of higher, associational processes and was called the 'visuo-psychic' band<sup>2</sup>. Such a terminology implied that 'sensation' occurred at the level of the striate cortex and 'perception' at that of the prestriate cortex.



**Fig. 1** Lateral view of the right hemisphere of the brain of rhesus monkey. The striate cortex (V1—vertical stripes) is situated posteriorly and ends 2 mm behind the lunate sulcus on the lateral side. The prestriate cortex (horizontal stripes) lies in front of the lunate sulcus and includes the depths of the deep sulci. Its anterior boundary is uncertain and it merges into the inferior temporal cortex (cross hatched), which is known also to have a visual function.

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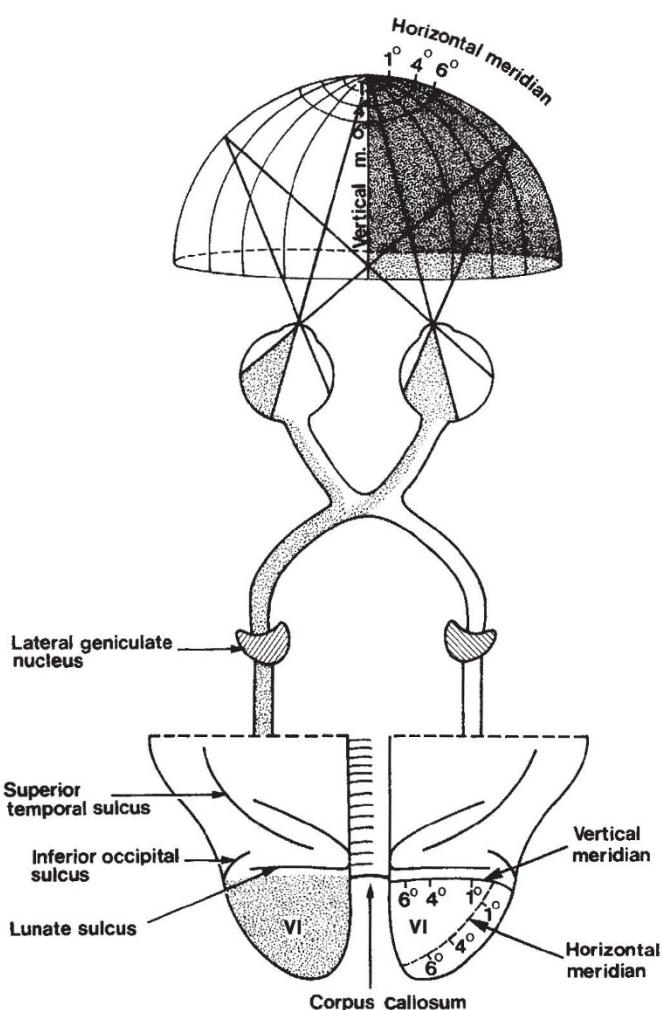
Such theories were vague and ill formulated, especially when viewed in the light of more modern anatomical and functional evidence. This evidence has shown that the prestriate cortex, far from being the single cortical field that its cyto-architecture might suggest, is in fact composed of several distinct visual areas<sup>12-15</sup>. Each of these has its own specific anatomical connections and in each one the visual fields are separately mapped, in characteristic ways. Extensive mapping experiments have revealed that a multiplicity of visual areas exists in the cortex of other species of monkey as well<sup>16-21</sup>. It is obviously of interest to know the reasons for having so many different visual areas. But in order to investigate their functional characteristics, it is necessary to define their boundaries. This is a difficult task in a field of uniform cytoarchitecture. But it is a difficulty that must be overcome if one wishes to study functional localisation within the visual cortex. Fortunately, this can now be done.

## Callosal connections as a guide to the visual areas

Because of the manner in which optic nerve fibres cross at the optic chiasm, it is the contralateral visual hemi-field that is represented in the striate area of each hemisphere<sup>6,7</sup> and in each visual area of the prestriate cortex<sup>22-25</sup> (Fig. 2). The visual field representation, separated into two hemifields by the chiasmatic crossings, is reunited in each visual area by the fibres of the corpus callosum<sup>15,26-29</sup>. This is a massive commissure linking the two halves of the brain. Because the visual hemifields, including the vertical meridian, are separately represented in each area, the existence of several distinct patches of callosally connected prestriate cortex<sup>29</sup> is good evidence that there are several distinct visual areas. Each callosal patch belongs to the vertical meridian representation of a separate visual area. That this is indeed so can be shown directly by simple experiments which combine anatomical and physiological techniques<sup>15,27,28</sup> (Fig. 3). The corpus callosum is sectioned six days before an electrophysiological recording experiment, a survival time which allows the cut callosal fibres to degenerate. Multiple electrode penetrations are then made in the prestriate cortex and the receptive field positions of cells in the different penetrations carefully noted. At the end of the experiment, the animal is killed and the brain sectioned and stained by a method which shows up the degenerated callosal fibres as well as the electrode tracks. It is found that cells lying in regions of the prestriate cortex where there is no degeneration and which, therefore, are devoid of callosal connections, have receptive fields distant from the vertical meridian. By contrast, cells in parts of the prestriate cortex which are callosally connected have receptive fields at, or extending to, the vertical meridian<sup>15,28</sup>.

As the vertical meridian is represented at one or more boundaries of the visual areas in the prestriate cortex<sup>12,13,30,31</sup>, the callosal patches also help in defining the boundaries of these areas. When recording from these areas, therefore, it is often sufficient to note the position of the electrode track with respect to the callosal degeneration to be able to state, with simplicity and certainty, which prestriate area one is recording from<sup>15,27,28,31</sup>. But neither the boundaries of the areas, nor the callosal patches, bear any constant relationship to gross structural frontiers, such as the depth of sulci<sup>29,31</sup>. Hence this approach of correlating positions of electrode tracks to the borders of the visual areas, seen through their callosal connections, is not a reprieve from the arduous task of making detailed reconstructions of the prestriate cortex for every recording experiment, but rather a confirmation that such reconstructions are mandatory.

This approach is also of great help in studying the connectivity of the different visual areas in the cortex. In such studies, one can inject labelled amino acids (which are taken up by nerve cells and transported to the terminals of their axons) into the prestriate cortex of animals whose corpus callosum had



**Fig. 2** Diagrammatic representation of the projections of the visual pathways, from retina to cortex, in the rhesus monkey. The temporal retina of the left eye projects to the left hemisphere, that of the right eye to the right hemisphere. The nasal hemi-retinas project to the contralateral hemispheres. Regions of vertical meridian representation in the visual areas of the cortex are callosally connected, but these are not shown in the diagram. Only the posterior part of each hemisphere, as viewed from above is shown.

been sectioned<sup>25,30,32</sup>. One can then tell which cortical area the injection was made into and which cortical area the label appears in, merely by noting the site of injection and label distribution in relation to the bands of callosal degeneration defining the boundaries of the areas.

What else do these callosal patches tell us about the visual areas? Some of the callosal patches, such as the one at the V1-V2 boundary, are narrow while others, such as the one within V4, are broad<sup>29,31</sup>. When such broad patches are reconstructed from section to section, one often notices a surprising variation in the density of degeneration within the callosal patch, with bands of heavy degeneration surrounding islands containing few or no degenerated fibres<sup>29,31</sup>. As the callosal connections are indicative of vertical meridian representation, what is one to make of such a picture? Does it indicate further differentiation into more areas, or a set of sub-areas?

## Definition of a visual area

There are at least five criteria which can be used to define a visual area. All these criteria can be applied to the striate cortex. They are (1) a well defined cytoarchitecture; (2) a complete map of the visual field; (3) a well defined anatomical input (in the case of the striate cortex an exclusive input from

the lateral geniculate nucleus); (4) distinct functional properties and (5) callosal connections.

Not all of these criteria can be used for identifying other visual areas, however. It is obvious that cytoarchitecture cannot be used to distinguish the prestriate areas from one another, as they all lie within a cortical region of uniform cytoarchitecture. Of the remaining criteria, the maps of the visual field are especially problematic. At the simplest level, one might consider that the visual field must be completely mapped once in a visual area. This is indeed so for the striate cortex<sup>6,7</sup>. But in other areas, the same part of the visual field may be multiply represented, or only the central part of the visual field may be represented. These variations presumably depend upon the functions of the areas. Hence visual field maps do not form a constant criterion with which to define areas. Indeed, they can even be misleading.

### Topographic maps in the cortex

A topographic map is a means of representing the body surface (in our case, the retina) in a certain order on the cerebral cortex. The order in which the retina is mapped on the cortical surface must bear a relation to the function of the area in question. Hence cortical maps are not all precise, geographic reproductions of the retinal surface, but are distorted in accordance with the functions of the areas. In the striate cortex, a proportionately larger amount of cortex is devoted to the fovea than to peripheral retina<sup>7,33</sup>. This is not surprising. One of the major functions of the striate cortex is to analyse contours in the visual field<sup>8</sup> and it is at the fovea that acuity is highest. Hence the need to distort the map in order to give the fovea greater and the periphery of the retina less representation, as in a distorting mirror. In spite of these distortions, continuity is maintained in the sense that adjacent points in the visual fields are represented at adjacent points in the striate cortex, which makes sense for an area analysing in detail orientations in visual space.

In V1, as well as in the two prestriate areas V2 and V3, the visual fields are separately mapped in a manner characteristic of the areas<sup>12,13</sup>. The topography in all these three areas is predictable and, if one were to record from the posterior bank of the lunate sulcus, starting at the V1-V2 boundary and then proceed medially to the depth of the sulcus, and then laterally, receptive fields of successive cells would move from the vertical to the horizontal meridian and then back again to the vertical meridian (Fig. 3)<sup>12,13,28</sup>. At the point of reversal, receptive fields suddenly change to larger (in V3) than in V2<sup>28,31</sup>. In this instance, the reversal in the topographic map alone is indicative of two different areas although, of course, there is supporting anatomical<sup>12,25,30</sup>, and electrophysiological<sup>25</sup> evidence to support such a delineation.

Reversals of this kind, when accompanied by changes in the properties of cells, or by differences in anatomical wiring, are acceptable evidence for boundaries between areas. But the functions of an area may dictate that the same part of the visual field must be multiply represented within it. In such an instance there would be several reversals in visual field representation within one area. There is therefore no reason to suppose that every reversal is indicative of a different visual area, nor that the visual fields need be mapped with the same degree of precision or distortion in areas with different functional properties. The motion area of the superior temporal sulcus, an area rich in directionally selective cells<sup>22,23</sup> can be taken as an example in which the visual field map is organised in a different way and in which, unlike V1, V2 or V3, the same parts of the visual fields are multiply represented. Evidently its functions require this. In this area several reversals in receptive field positions sometimes occur even in a single penetration sampling tangentially from not more than 3 mm of cortex. Figure 4 shows this. Between cells 1 and 10, a total distance of less than 2 mm, receptive fields of cells move from a position 25° below and 25° contralateral to the vertical meridian (at 1) to the vertical meridian above the horizontal meridian (at 6), then

reverse to a position below the horizontal meridian (at 7), only to go up again at 11, and then move down once again at 20. Although the reversals are frequent, the functional properties of the cells do not change, all of them being directionally selective. It seems reasonable to consider it, therefore, as a single visual area in which the same parts of the visual fields are multiply re-represented and which has, therefore, a map of the visual field radically different from those of V1, V2, V3 and V3A—different because the functions of the area, in this case motion analysis, are different.

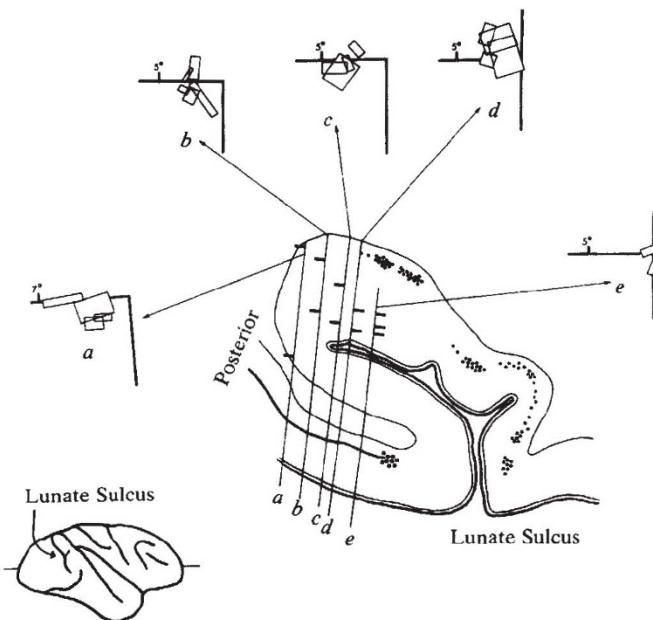
In both the motion area, and in V4 (ref. 31), the same part of the visual field, including the vertical meridian, is multiply represented. As regions of vertical meridian representation are callosally connected, it is hardly surprising to find that both have patchy and complex patterns of callosal connections, compared to those of V2 and V3 (refs. 29,31). The pattern of callosal connectivity is dictated by the manner in which the visual field is represented in an area. This in turn depends upon the function of the area. The function, finally, is dictated by the anatomical input. Hence, functional properties and anatomical inputs are the best criteria for defining an area.

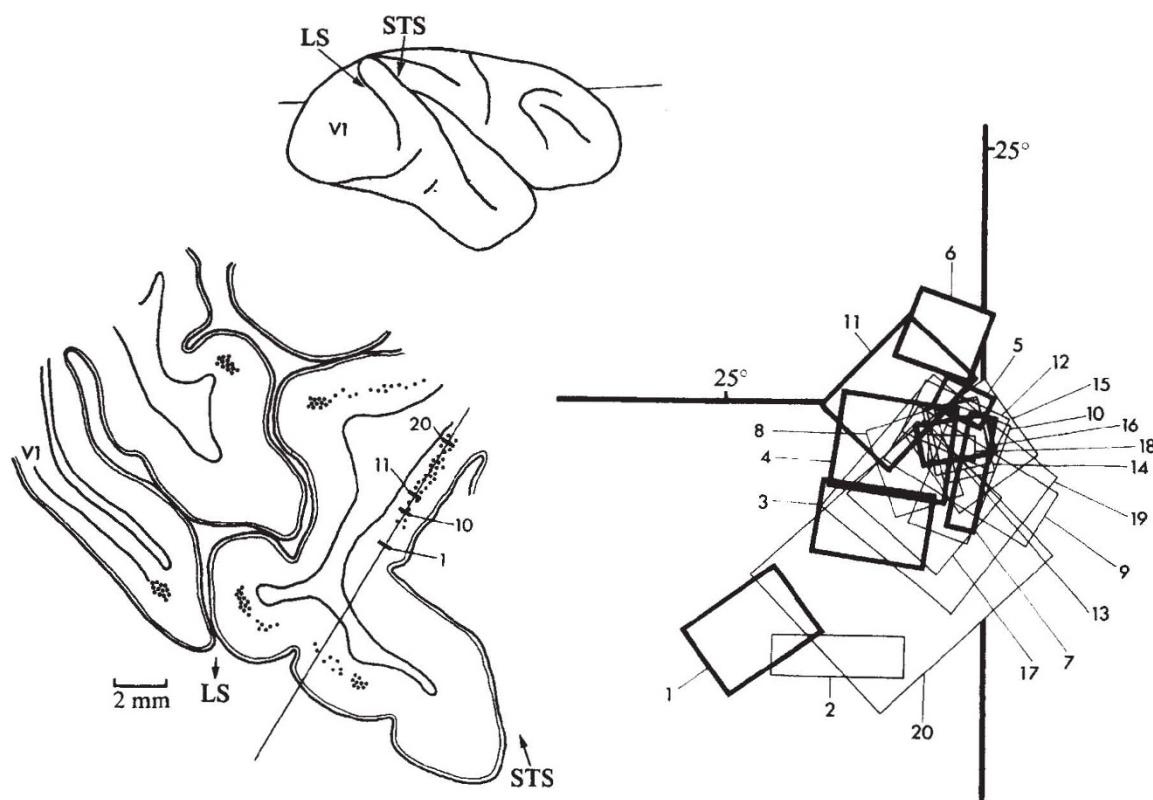
Despite these qualifications, it is always best to consider all five criteria in deciding whether to confer the status of an area on a region of the visual cortex. An area such as V3A, for example, has a map of the visual field that is so predictable and different from other areas that one has to consider it as an independent area<sup>31</sup>, even if there is no compelling difference, to date, in the functional properties of cells between it and one of the two neighbouring areas, namely V3 (ref. 25).

### The number of prestriate areas

Considering all the criteria given above, one can divide the prestriate cortex into at least six different areas (Fig. 5). All these areas, except the motion area of the superior temporal

**Fig. 3** Reconstruction of five parallel horizontal penetrations through the lunate sulcus of a monkey whose corpus callosum had been sectioned 6 days before the recording experiment. The dots in the cortex represent callosal fibre degeneration. The penetrations were made at the level indicated on the drawing of the brain to the lower left. In the penetrations *a*-*e*, the short horizontal lines intersecting the electrode track indicate the region from which recordings were made. Receptive fields of groups of cells in each penetration are separately indicated in the plots *a*-*e*. Note that receptive fields of cells in regions where there is no degeneration lie away from the vertical meridian, whereas in regions of degeneration receptive fields are at the midline. (From ref. 28.)





**Fig. 4** Reconstruction of an experiment in which a long electrode penetration was made through the cortex of the medial part of the posterior bank of the superior temporal sulcus. To the left is a tracing of a horizontal section, taken at the level indicated on the surface drawing of the brain. The first 10 cells were situated in the region of the track enclosed by the two short horizontal bars, marked 1 and 10, intersecting the common electrode track and cells 11–20 were situated in the region marked by the corresponding horizontal bars. Conventions as in previous figures. The receptive fields of the individual cells are separately plotted to the right of the figure. Note that in the progression from 1 to 10, receptive fields move from the lower quadrant (1), to the centre of gaze and the vertical meridian (5), the superior quadrant (6) and then back down to the inferior quadrant (7), only to reverse again at 11, and yet again at 20. Note also that the first four cells, not being in a region of the cortex with callosal connections (as shown by the absence of degeneration) had receptive fields well away from the vertical meridian, whereas the remaining cells, being in regions of callosal degeneration, had receptive field extending to the vertical meridian. LS, lunate sulcus; STS, superior temporal sulcus.

sulcus, lie within Brodmann's cytoarchitectonic area 18 (ref. 3). Starting posteriorly at the border of V1, these are V2, V3 (refs 12, 13) and V3A (refs 25, 31), each one of which is identifiable as a separate visual area by (1) its distinct anatomical inputs; (2) its separate callosal connections; and (3) the separate, distinctive and topographic map of the visual field within each area. As well, although most cells in V2 and V3 are orientation selective<sup>34</sup>, V3 cells have larger receptive fields than V2 cells at comparable eccentricities<sup>28,31</sup>. This difference alone enables one to state with certainty the transition from V2 to V3 in a single penetration. It is, however, more difficult to distinguish between V3 and V3A on the basis of the properties of single cells, as studied to date<sup>25</sup>. Most cells in both areas are orientation selective and there is no sharp difference in receptive field sizes at equivalent eccentricities, as there is between V2 and V3<sup>25</sup>. Nevertheless, the different, and distinctive map of the visual field within V3A, compared to other areas, as well as its distinctive anatomical input<sup>25</sup> and callosal connections<sup>25,31</sup>, make of it an independent visual cortical area.

Lying lateral to V3A in the lunate sulcus, and extending on to the prelunate gyrus, and then the lateral part of the posterior bank of the superior temporal sulcus is a zone of cortex, which can be subdivided into a posterior area with its distinctive anatomical and callosal connections<sup>14</sup> and an anterior area, which also has its separate anatomical and callosal connections<sup>15</sup>. The visual fields are separately mapped in each area in a complicated way, the same part of the visual field being multiply represented within each area. Because the properties of the cells in the two areas are so similar (see below) I group them

together as the areas of the fourth visual complex<sup>15,34</sup> (V4). The reason for not naming these areas further is that details concerning their common borders remain to be settled. There are suggestions from the anatomy that it may be possible to subdivide each area<sup>14,15</sup>.

Lying more medially within the posterior bank of the superior temporal sulcus is another visual area, recognisable as an independent area by its distinct anatomical and callosal connections and by its distinct functional properties<sup>22,23</sup>. For the present, I refer to it as the motion area.

### Functional specialisation within the visual cortex

The callosal landmarks allow one to overcome the problem of defining the boundaries of the visual areas. One can now record from single cells in these areas and compare the response of cells in one area with those in another. Fortunately, there are no obvious differences in the properties of single cells when one compares recordings made from intact brains with recordings made from brains with a sectioned corpus callosum<sup>15,25</sup>. Hence sectioning the corpus callosum provides useful anatomical guides to the borders of the cortical areas without interfering with the properties of single cells.

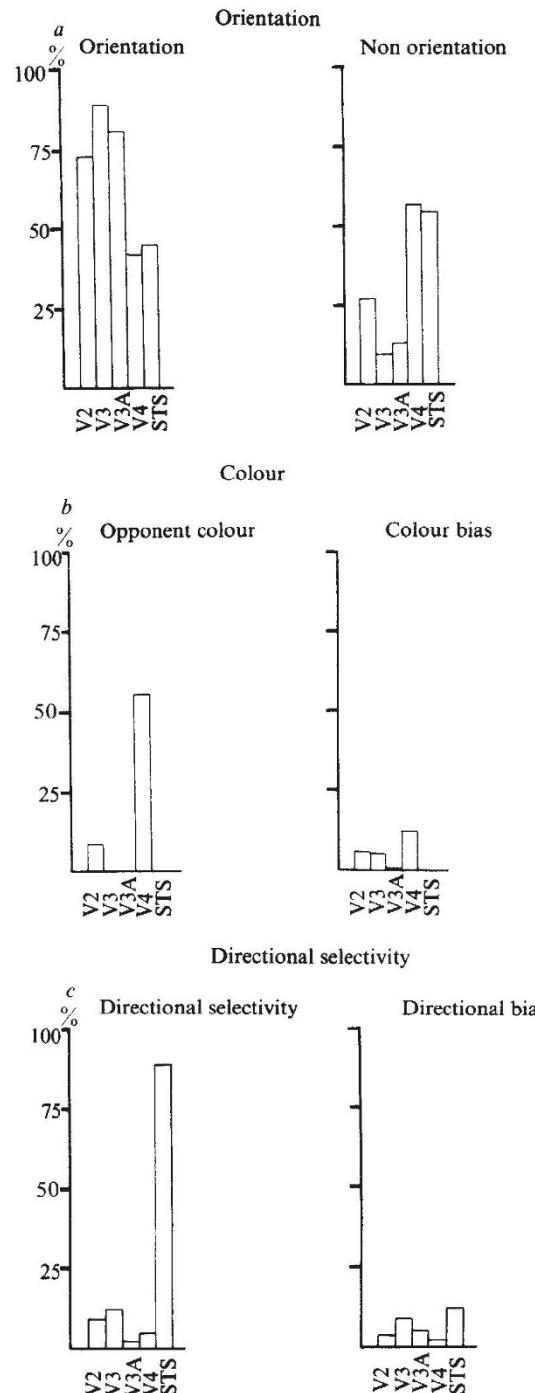
Recordings made from 1,500 single cells in the prestriate cortex<sup>34</sup>, summarised in Fig. 6, reveal differences in the distribution of orientation, colour, and motion selective cells in the different cortical areas. Most orientation selective cells are grouped into three areas—V2, V3 and V3A. Significantly,

receptive field sizes of cells are smaller in V2 than in V3 or V3A at equivalent eccentricities<sup>28,31</sup>. Colour specific cells (that is, those responding to one part of the spectrum and not to other parts or to white light, or those excited by one part of the spectrum and inhibited by another) are grouped into the areas of the V4 complex<sup>34</sup>. The percentage of orientation selective cells in the areas of the V4 complex is significantly lower than those in V2, V3 or V3A. Finally, the directionally selective cells (that is those responding to motion of the visual stimulus in one direction only) are found in heavy concentrations in the motion area of the superior temporal sulcus<sup>34</sup>. Even orientation selective cells here are also directionally selective<sup>22</sup>. This positive evidence is as compelling as the negative evidence. For example, there is no hint of colour coded cells in V3 or V3A, or in the motion area, and only a small proportion of directionally selective cells in V2, V3, V3A or the areas of the V4 complex. It is obvious that these different areas do not analyse the same features of the visual environment at an ever increasing complexity, but rather that they analyse different types of information in the visual environment.

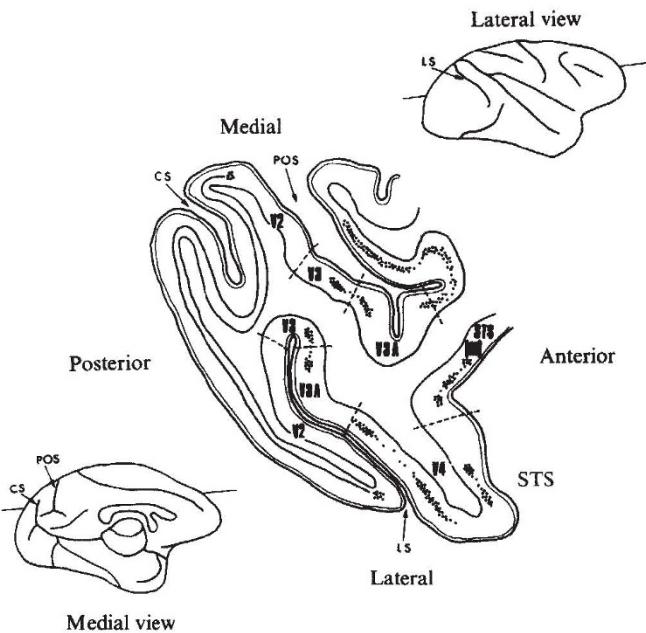
Paradoxically, these very differences in the type of information analysed by the different prestriate areas must impose certain similarities on them. If different prestriate areas are to analyse different types of information contained in the same part of the visual field, the same part of the visual field must be represented in each area. This is indeed the case. But one would not expect the same extent of the visual field to be mapped in each area. There would be little reason to map the far periphery of the visual field in an area which is concerned with analysing colour in the visual field since colour perception is best in the central 20° and absent in the far periphery. By contrast, there is every reason to represent the peripheral visual field in the motion area since displacements in the peripheral field are powerful visual stimuli. Hence the failure to identify any representation of the visual field beyond 20° in

V4<sup>15,24</sup>; hence also the powerful representation of the periphery in the motion area of the superior temporal sulcus (S.M.Z., unpublished). Variations in the extent of the visual field represented in different prestriate areas have also been reported for other species of monkeys<sup>21</sup>. Hence the differences in function between the different areas are superimposed upon common features. Anatomically, the common feature is a uniform cytoarchitecture upon which differences are superimposed by different anatomical inputs<sup>32</sup>. Functionally, the common feature is the re-representation of the same part of the visual fields and of the two eyes in every area<sup>34</sup>, the differences being that in every area a different type of information is analysed. Thus our present-day knowledge of the organisation

**Fig. 6** The percentage distribution of orientation selective (*a*), colour selective (*b*) and directionally selective (*c*) cells in the prestriate areas.



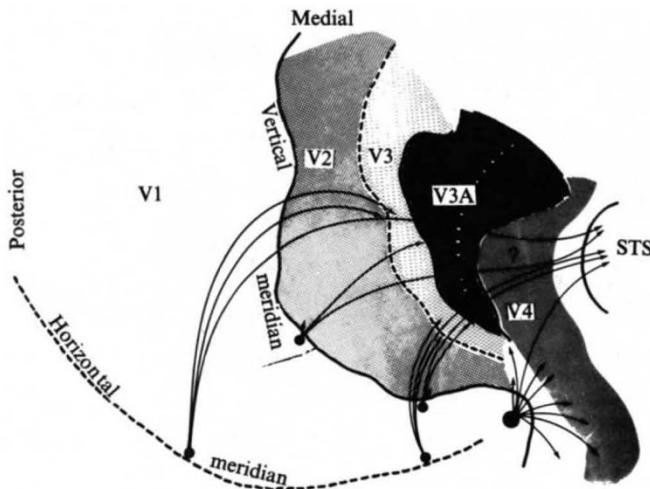
**Fig. 5** A tracing of a horizontal section through the striate and prestriate cortex, at the levels indicated on the medial (left) and lateral (above, right) surface drawings of the brain of an animal in which the corpus callosum had been sectioned. The degeneration following such a section is represented as dots. Note that the callosal patches can be narrow (as at the V1-V2 boundary) or broad and patchy (as in V4) and in the medial part (STS M) of the superior temporal sulcus. The callosal landmarks indicate that several distinct visual areas must exist within a single cyto-architectonic field. The boundaries of the areas are indicated by interrupted lines. Continuous line in the cortex represents VI. LS, lunate sulcus; STS, superior temporal sulcus.



of the visual cortex goes some way to support theories of cortical localisation of function which the early neurologists fought so hard to establish<sup>35</sup>. It would, of course, be naive to suppose that the kind of functional specialisation revealed in these studies implies that every visual area has one function only. Future, more sophisticated, studies may well reveal other functions for each visual area.

What does this kind of anatomical and functional organisation reveal about the cortical processes involved in vision? It tells us that the theory of a visuo-sensory cortex limited to the striate cortex, and a visuo-psychic band incorporating the prestriate cortex is almost certainly false, because the sensory analysis of the visual environment is far from complete at the level of the striate cortex. It tells us, instead, that there are several strategies that the cortex utilises concurrently in analysing the visual environment. One strategy is for each area to act not only as an integrator of the information coming to it, but also as a distributor of information, sending different types of information to different visual areas for further analysis<sup>27,32</sup>. Nowhere is this more evident than in the striate cortex. All the information in the retino-geniculo-cortical system passes through the striate cortex. The striate cortex, in turn, sends distinct outputs to different prestriate areas<sup>27,32</sup> (Fig. 7). It would be difficult to imagine that it sends the same information to these different areas. Differences in the properties of cells in the different prestriate areas to which it projects confirm that it does not. But it must not be imagined that this information is necessarily relayed in a passive way. Rather, much of the information, but perhaps not all, is elaborated before being relayed. For example, the striate cortex combines the information coming from the two eyes<sup>8</sup>. It also uses the information provided by the centre-surround cells of the lateral geniculate nucleus to provide information about orientation<sup>8</sup>. It then passes this information on orientation selectivity to other prestriate areas, whose cells are mostly binocularly driven<sup>34</sup>, and generalises it over greater or lesser extents of the visual field in the different prestriate areas. Such a double role of integration and distribution may also be postulated for other prestriate areas, as each prestriate area, in turn, projects to more than one further area<sup>14</sup>.

**Fig. 7** Summary diagram of the projections of the striate cortex, displayed on a 'flattened out' striate and prestriate cortex. Only the projections of the part of the striate cortex representing lower visual fields are shown, but the part of the striate cortex representing upper visual fields has similar projections. Interrupted lines indicate the representation of the horizontal meridian, continuous lines that of the vertical meridian. Note that each part of the striate cortex has direct projections to V2, V3 and the medial part of the posterior bank of the superior temporal sulcus (STS). The region of the striate cortex at which the centre of gaze is represented has an additional projection—to V4. (From ref. 34.)



This strategy of analysis and integration of information, and the distribution of information, tells us of two further strategies that the visual cortex uses in analysing the visual environment. One is the simultaneous analysis of different types of visual information in the different areas—hence the need to represent the visual field separately in each area. Another strategy is a hierarchical one, the information analysed in one area being used in another, more central, area in a more complex fashion. For example, the truly binocular, orientation selective cells of V2<sup>34</sup> use the information provided by the orientation selective cells of V1 which, however, are not truly binocular, but prefer one eye<sup>8</sup>. In this hierarchical system, receptive fields of cells in V2 are larger than those in V1, at comparable eccentricities, just as the fields of cells in V3 (which also receives a direct input from V1)<sup>12,13</sup> are larger than those in V2. In such a progression, orientation selectivity is generalised over ever wider parts of the visual fields.

The picture of the visual cortex that we have today, then, is one of a large cortical field containing several different visual areas. These have some features in common such as analysing the same parts of the visual fields, and yet differ in being functionally specialised to analyse different features in the same part of the visual field. Our picture of the prestriate cortex is obviously far from complete. Much of it, especially on the medial side of the brain, remains unexplored and there are powerful hints from anatomical studies that yet further distinct visual areas may be found<sup>14,15,36</sup>. Moreover, the details of how an area, such as V4, analyses information relating to colour remain far from settled. Questions also remain concerning functional specialisation for other attributes, such as depth detection<sup>37,38</sup>. Finally, one is naturally very curious to learn how the information analysed in different areas of the prestriate cortex is then used to give a unitary 'perception' of the visual world. Much exciting work remains to be done, therefore, and to this extent the work done to date is no more than a beginning. But it is gratifying to know that by using relatively simple anatomical and electrophysiological techniques one has every hope of beginning to acquire an understanding of what is undoubtedly the most mysterious and interesting part of the body—the cerebral cortex.

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