J. Physiol. (1978), **277**, *pp.* 227–244
With 1 *plate and* 10 *text-figures*
Printed in Great Britain

THE CORTICAL PROJECTIONS OF FOVEAL STRIATE CORTEX IN THE RHESUS MONKEY

By S. M. ZEKI*

From the Department of Anatomy, University College London, London WC1E 6BT

(*Received 31 March 1977*)

SUMMARY

1. The cortical projections of the foveal and extrafoveal parts of the striate cortex have been compared, using conventional degeneration techniques, as well as combinations of anatomical methods. While both foveal and extrafoveal striate cortex share a common pattern of projections (to areas V2, V3 and the visual area in the medial part of the posterior bank of the superior temporal sulcus), foveal striate cortex was found to have an additional projection (to part of the cortex of the fourth visual areas, V4). The latter projection includes the posterior lip of the inferior occipital sulcus which, on anatomical grounds, is regarded as the ventral extension of V4.

2. Anatomical studies using double tracers were employed to clarify the nature of the projections from the striate cortex and from V2 to V4. In one such experiment, tritiated proline was injected into extra-foveal striate cortex and a small lesion was made in that part of V2 receiving a direct projection from the region of the striate cortex into which the radioactive tracer was injected. Only degenerating fibres (due to the lesion), and no radioactive label, was found in V4. Such an experiment showed that, unlike foveal striate cortex, the projections from extrafoveal striate cortex to V4 are not direct, but through V2.

3. In another type of anatomical experiment using double tracers, the corpus callosum was sectioned and tritiated proline was injected into foveal striate cortex. Such an experiment allowed a more accurate determination of the extent of V4, as judged from its callosal connexions, to which foveal striate cortex projects.

4. Considering the projections of V1 to areas V2, V3 and the visual area in the medial part of the posterior bank of the superior temporal sulcus, and considering the differences in the projections of foveal and extrafoveal striate cortex, it is suggested that, among other functions, the striate cortex acts as a distribution centre for the information coming over the retino-geniculo-cortical pathways, parcelling this information out to different visual areas of the prestriate cortex for further analysis.

INTRODUCTION

The retina of the rhesus monkey is a remarkably non-uniform structure, with pronounced differences between its centre and periphery. Chief among these is the presence of a central area, the foveola, with its specialized anatomy, high acuity and

* Head Fellow of the Royal Society.

heavy concentration of cones (Østerberg, 1935). The density of ganglion cells and midget bipolars also falls off at increasing distances from the fovea (Van Buren, 1963; Boycott & Dowling, 1969). It would be surprising if this non-uniformity were not represented at more central levels of the visual pathways, since the retina projects in a point-to-point, topographic manner to the striate cortex (Talbot & Marshall, 1941; Daniel & Whitteridge, 1961; Guld & Bertulis, 1976). Indeed, the unequal distribution of cones in the retina is reflected in the greater concentration of colour coded cells in foveal striate cortex (Dow & Gouras, 1973; Gouras, 1974) compared with more peripheral striate cortex (Hubel & Wiesel, 1968) and differences in the local connectivity of the retina are mirrored in the smaller receptive fields of cells situated in regions of central, compared to peripheral representation (Hubel & Wiesel, 1974).

The striate cortex, which is the first cortical stage for the retino-geniculo-cortical system, projects to different visual areas in the prestriate cortex which surrounds it (Zeki, 1969; Cragg, 1969). This paper addresses itself to the following question: Do the projections of foveal striate cortex on to the prestriate cortex differ in any way, either quantitatively or qualitatively, from those of non-foveal striate cortex? The differences could be only quantitative, with foveal striate cortex claiming more or less territory within each area, thus leading to nothing more than changes in magnification factors (Daniel & Whitteridge, 1961) in the different areas. But given the heavy cone representation within foveal striate cortex, the differences could be more pronounced. That is why these projections were compared.

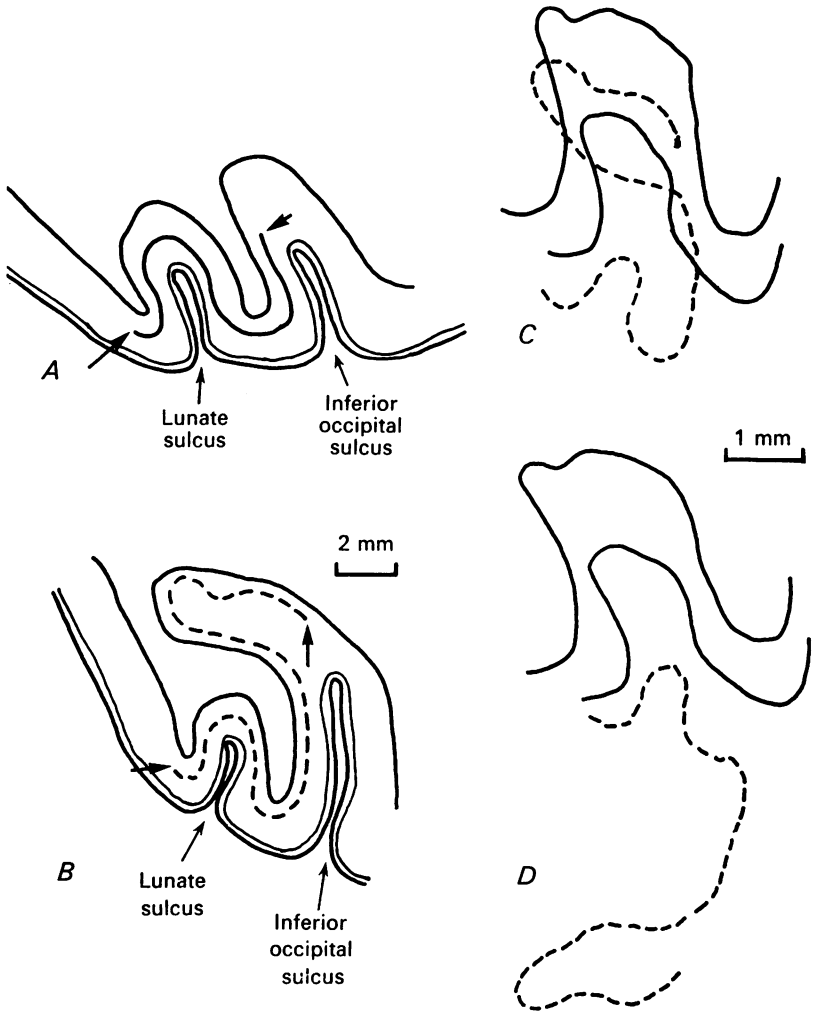
METHODS

Several different techniques were used in the present study. One method of studying the projections of foveal striate cortex was the conventional one of making a small lesion in this region by subpial suction (Zeki, 1969). The animals were sacrificed 8–10 days after surgery by transcardial perfusion with normal saline followed by a 4% solution of buffered paraformaldehyde and the brains were sectioned and stained for degenerating fibres by the Wittanen (1969) method. Often, double tracer anatomical methods were used (Zeki, 1976, 1977*b*). For example, to demonstrate convincingly that there is a difference in the projection of foveal, as opposed to non-foveal, striate cortex, lesions were made in the former 8 days before sacrifice and a labelled amino acid was injected into non-foveal striate cortex of the same hemisphere 2 days before sacrifice. The labelled amino acid chosen for this purpose was tritiated proline and the injection was done according to procedures already described (Zeki, 1976). Following sacrifice, the brain was sectioned horizontally, alternate sections being 20 and 40 μm thick. The thinner set was mounted on gelatinized slides and then treated for autoradiographic label following the procedures described by Cowan *et al.* (1972), while the thicker set was stained for degenerating fibres. Double tracer methods were also used to compare the projections from V1 and V2 on to the anterior bank of the lunate sulcus and the procedures used in these experiments were identical to what is described above.

In another type of anatomical experiment using double tracers, the splenium of the corpus callosum was sectioned and, 2 days before sacrifice, labelled proline was injected into either foveal striate cortex or into V2. This was done because the distribution of the callosal fibre degeneration is a powerful anatomical guide to the boundaries of the different prestriate areas (Zeki, 1975; Zeki & Sandeman, 1976; Van Essen & Zeki, 1978), including V4. The brains were then sectioned, alternate sections being stained for degenerating fibres and treated for autoradiographic label in the manner described above. Such a procedure allowed one to study the distribution of the autoradiographic label in relation to the callosal bands that define different areas of the prestriate cortex, and hence the extent of V4 receiving an input from foveal striate cortex and from V2.

In making lesions in the part of the striate cortex at which the foveola (the central, rod-free

part of the retina) is represented, the map of Daniel & Whitteridge (1961) and Guld & Bertulis (1976) was used. In the latter map, the representation of the central 0–4° of the visual field is plotted in detail and comparison of the site of foveal lesions with that map shows that the lesions must have been made within the part of the striate cortex in which the central 0–0·5° is represented. Recordings were not undertaken before making the lesions to establish whether the foveola is represented at this region in every animal. It is, of course, possible that there may be some variability from animal to animal in the exact position at which the fovea is represented. This would seem unlikely since in every case where a foveal striate lesion was made, the pattern of degeneration was similar and included degeneration in areas to which non-foveal striate cortex does not project.



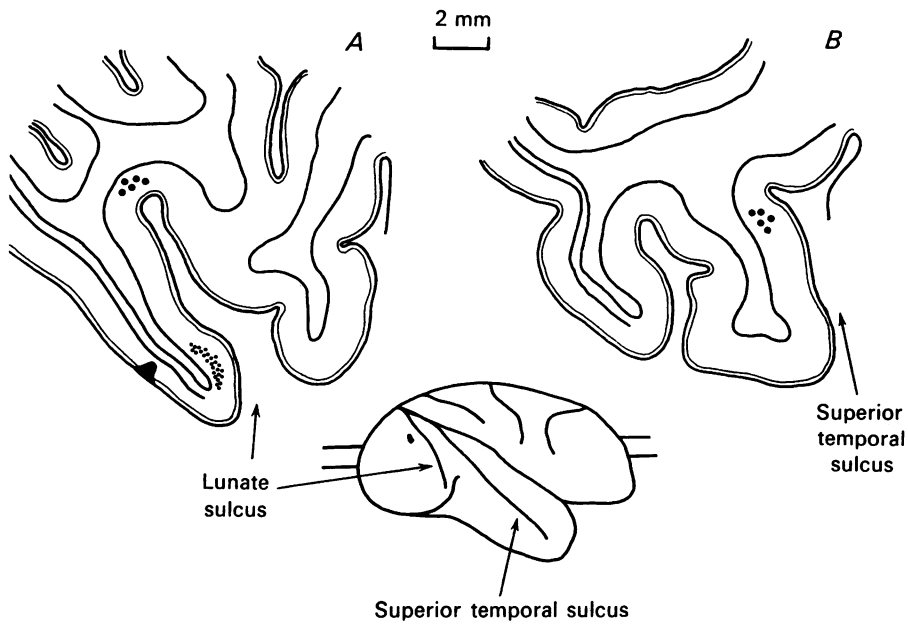
Text-fig. 1. Diagram to illustrate the manner in which the contour lines for the lunate sulcus (continuous lines) and the inferior occipital sulcus (interrupted lines) would cross if the contour lines for both sulci were to be drawn at the same orientation and aligned against each other (as in *C*). This cross over can be avoided by drawing the mirror image of the contour line for the inferior occipital sulcus (as in *D*). *A* and *B* are tracings of horizontal sections at levels at which the lunate sulcus becomes shallow and the inferior occipital sulcus increases in depth. The continuous and dashed lines (between the arrows) in the two sections are the contour lines reconstructed to the right (see also Text-fig. 5).

Cortical reconstructions. The method of reconstructing the prestriate cortex in detail is described in a companion paper (Van Essen & Zeki, 1978). However, because the degeneration following foveal striate lesions involves the posterior bank of the inferior occipital sulcus, in addition to the anterior bank of the lunate sulcus, the reconstructions are taken to more ventral levels than in the previous paper. This posed a problem, for to continue drawing the contour lines as the lunate sulcus ends and the inferior occipital sulcus begins and deepens would mean that the two sets of contour lines, one set for the lunate sulcus, the other for the inferior occipital, would cross (see Text-fig. 1). This problem could be overcome, however, by reversing the contour lines of the inferior occipital sulcus (i.e. drawing its mirror image) with respect to those of the lunate sulcus (see Text-fig. 1). This procedure had the advantage of displaying the continuity in the degeneration between the anterior bank of the lunate sulcus and the posterior lip of the inferior occipital sulcus, without introducing any significant distortions beyond what is described in the previous paper.

Note on terminology. In this paper, the terms striate cortex, V1 and area 17 are used interchangeably.

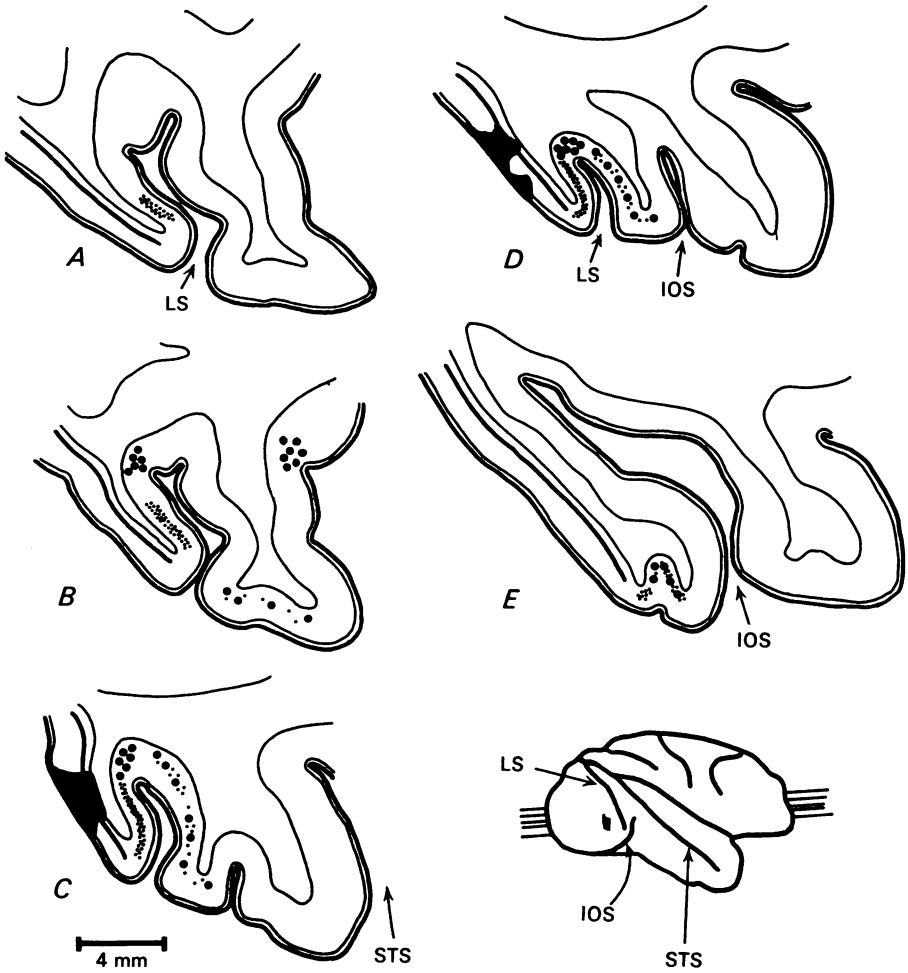
RESULTS

The degeneration following extrafoveal lesions of striate cortex has been described before (Cragg, 1969; Zeki, 1969). In brief, a lesion made in the striate cortex, in a region representing the vertical meridian of the visual field at about 3° below the centre of gaze, results in three separate patches of degeneration in the prestriate cortex, a region of fine degeneration at the posterior lip of the lunate sulcus (V2),



Text-fig. 2. Reconstructions of an anatomical experiment in which a lesion was made in area 17 (V1) in the region of vertical meridian representation at about 3° from the centre of gaze. The lesion is shown in solid black. *A* and *B* are tracings of horizontal sections, taken at the levels indicated on the surface drawing of the brain, to show the distribution of the degeneration following such a lesion. Note the presence of fine degeneration (small dots) in the posterior bank of the lunate sulcus and coarse degeneration (large dots) in the depth of this sulcus as well as in the posterior bank of the superior temporal sulcus. Note also the absence of degeneration in the anterior bank of the lunate sulcus. Continuous line in the cortex indicates V1.

a region of coarse degeneration in its depth (V3), and a third one in the movement area of the posterior bank of the superior temporal sulcus (see Text-fig. 2). A lesion made in the striate cortex, in a region representing the vertical meridian at about 2° above the centre of gaze, also results in three separate patches of degeneration, but

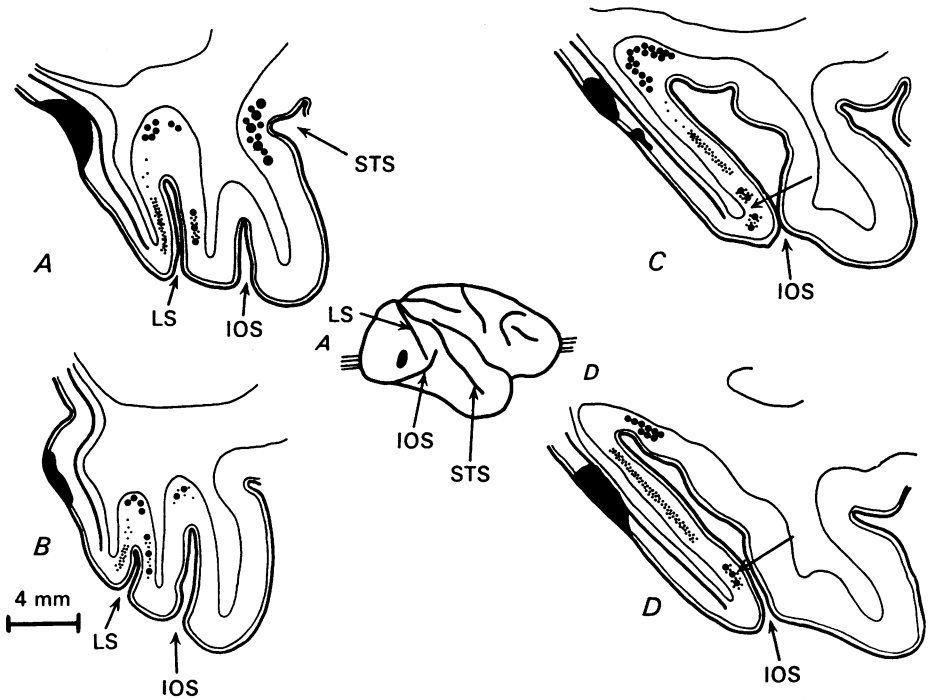


Text-fig. 3. Reconstructions of an anatomical experiment in which a small lesion was made in the region of foveal representation of V1 according to the maps of Guld & Bertulis (1976) and Daniel & Whitteridge (1961). Conventions as in Text-fig. 2. Note the fine and coarse degeneration in the posterior bank and depth of the lunate sulcus, as well as the coarse degeneration in the posterior bank of the superior temporal sulcus. In addition to this pattern of projections, which foveal striate cortex shares in common with extrafoveal striate cortex (Text-fig. 2) there was degeneration in the anterior bank of the lunate sulcus as well as on the surface of the prelunate gyrus (see sections *B–E*). IOS, inferior occipital sulcus; LS, lunate sulcus; STS, superior temporal sulcus.

these fall at the posterior lip of the inferior occipital sulcus (V2), in its depth (V3) and in the movement area of the posterior bank of the superior temporal sulcus, the upper and lower visual quadrants being separately represented in areas V2 and V3 (Zeki, 1969; Cragg, 1969). Neither lesion produces any degeneration in the lateral two thirds

of the anterior bank of the lunate sulcus where the fourth visual areas, rich in colour coded cells, are situated (Zeki, 1973, 1975).

Such a pattern of degeneration can be compared with the one following a lesion of equivalent size, also made in the striate cortex, but this time in the region of foveal representation (central 0·5°) according to the map of Guld & Bertulis (1976). Text-fig. 3 is a reconstruction of such an experiment. Note that the fine degeneration in



Text-fig. 4. Reconstruction of an anatomical experiment in which a foveal striate lesion, larger than the one shown in Text-fig. 3, was made. Conventions as in previous Figures. *A–D*, tracings of horizontal sections, taken at the levels indicated on the surface drawing of the brain in the centre. Note the presence of fine and coarse degeneration in the posterior bank and depth of the lunate (*A*, *B*) and inferior occipital (*C*, *D*) sulci and of degeneration in the posterior bank of the superior temporal sulcus (*A*). In addition to these patches there was also degeneration in the anterior bank of the lunate sulcus (sections *A* and *B*), the depth of the inferior occipital sulcus (IOS) at its inception (*B*) and, inferiorly, in the lateral part of the posterior bank of the inferior occipital sulcus (marked by arrows) a region to which the fourth visual areas can be directly traced (Zeki, 1970, 1971).

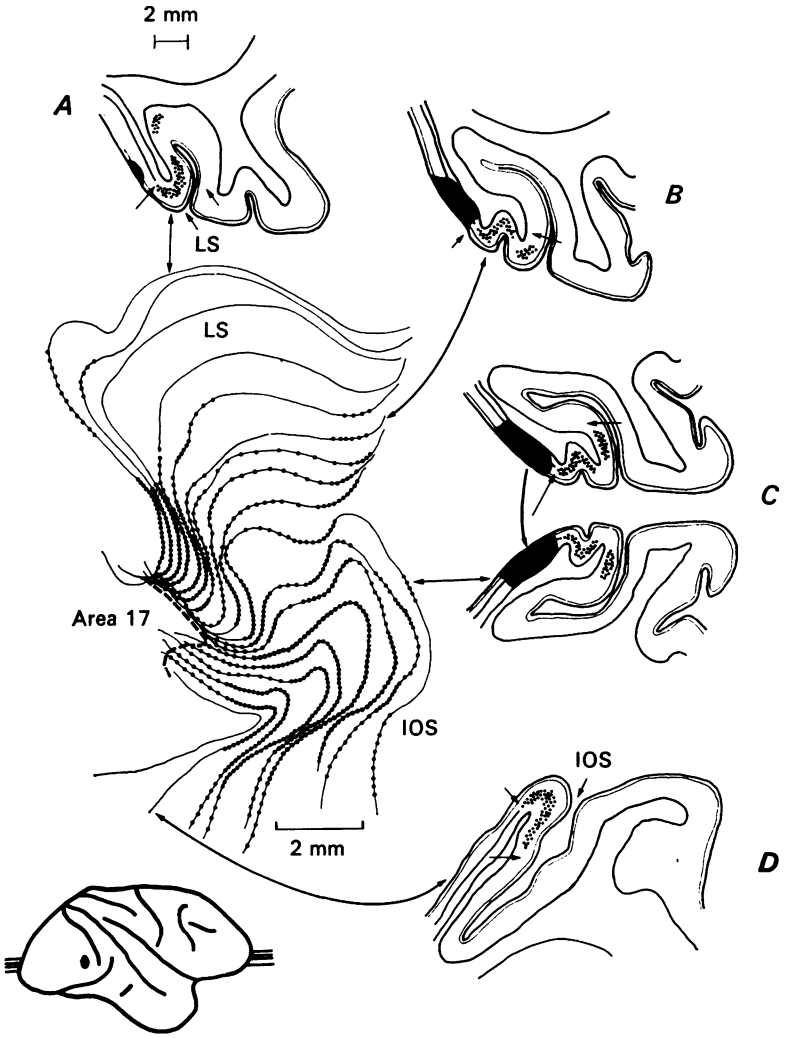
the posterior bank of the lunate sulcus, the coarse degeneration in its depth as well as the coarse degeneration in the posterior bank of the superior temporal sulcus were all manifest. It is therefore evident that foveal and extrafoveal striate cortex share, to a large extent, a common pattern of cortical projections. But, following a foveal striate lesion, the degeneration also spread over the anterior bank of the lunate sulcus, up to the prelunate gyrus, a distribution not seen with extrafoveal lesions. Both fine and coarse fibres appeared in this latter field of degeneration and the density

of degeneration increased as more ventral levels were examined, although it never matched the density at the posterior bank of the lunate sulcus (V2) (see Pl. 1).

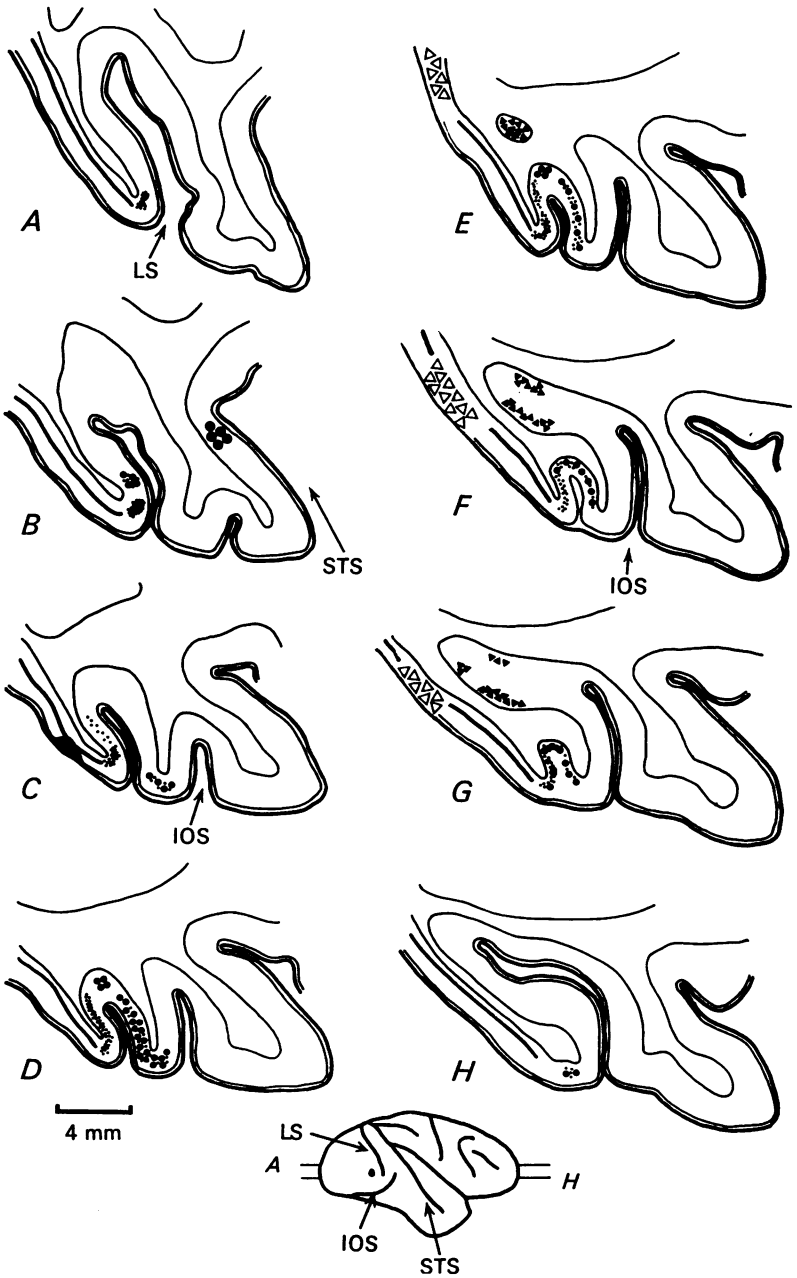
At the level of the lunate sulcus in which degeneration was found following foveal striate lesions (Text-fig. 3), much of its anterior bank is occupied by the fourth visual areas (Zeki, 1971; Van Essen & Zeki, 1978). Hence this part of the fourth visual area appears to receive a direct input from foveal striate cortex. When traced ventrally, this part of the fourth visual areas comes to occupy the lateral part of the posterior bank of the inferior occipital sulcus. This change occurs because of the complicated pattern of fissuration at this level, as is described in detail elsewhere (Zeki, 1971). The next experiment, illustrated in Text-fig. 4, shows that this ventral extension of the fourth visual areas also receives a direct input from foveal striate cortex. In this animal, in which the foveal striate cortex lesion extended further ventrally than the one shown in Text-fig. 3, there was degeneration in the posterior bank and depth of the lunate sulcus as well as in the posterior bank of the superior temporal sulcus. Degeneration also appeared, however, in the anterior bank of the lunate sulcus as well as at the posterior lip of the inferior occipital sulcus (marked by arrows). Two further areas of degeneration in the inferior occipital sulcus, a laterally situated field of fine degeneration and a more medially situated coarse one, almost certainly belong to the parts of V2 and V3 representing the upper visual fields, the lesion in the striate cortex presumably having invaded the area of representation of the upper visual fields (Cragg, 1969; Zeki, 1969).

Although such a pattern of projections confirmed that the ventral extension of the fourth visual areas also receives a direct input from foveal striate cortex, one wanted to have the satisfaction of seeing a direct continuity of degeneration from the anterior bank of the lunate sulcus to the posterior lip of the inferior occipital sulcus following a foveal striate lesion. Such a continuity is evident from the experiment illustrated in Text-fig. 5. In this animal a lesion was inflicted in foveal striate cortex and the brain sectioned and stained as before. However, a more detailed reconstruction of the degeneration in the prestriate cortex was made. Sections were taken at 500 μm intervals and the contour lines for each section were drawn and the degeneration filled in. Next, the contour lines from contiguous sections, 500 μm apart, were aligned one against the other on a sheet, as described in the methods section. The results showed a continuous belt of degeneration extending ventrally from the anterior bank of the lunate sulcus, where the fourth visual areas are situated, to the posterior lip of the inferior occipital sulcus, to which the ventral extension of V4 has been traced (Zeki, 1970, 1971 and see Text-fig. 5). Recordings made in the posterior lip of the inferior occipital sulcus, at the level at which the sulcus has become deep, as well as at its inception (which also receives an input from foveal striate cortex – see Text-fig. 4*B*) have shown that there are heavy concentrations of colour coded cells in these regions, comparable in properties to those in the part of V4 lying in the anterior bank of the lunate sulcus (S. M. Zeki, unpublished results).

In summary, then, it may be said that foveal striate cortex projects directly to the fourth visual complex, in addition to its projection to V2, the movement area of the posterior bank of the superior temporal sulcus and possibly V3 (as discussed in a companion paper, Zeki, 1978*a*). With lesions in non-foveal striate cortex, at 2–3° below the centre of gaze, I have *occasionally* observed a few fibres in the fourth visual



Text-fig. 5. Detailed reconstruction of the lunate and inferior occipital sulcus for an anatomical experiment in which a lesion was made in foveal striate cortex. Only the lateral part of the posterior bank of the inferior occipital sulcus is reconstructed. Contour lines of sections spaced by 500 μm intervals were drawn and the degeneration filled in for the contour of each section. The region of the sections for which contour lines were drawn are indicated by arrows in the representative sections *A–D*. The contour line of each section was deformed a little in order to be able to place it next to neighbouring contour lines without any crossover. The degree of unbending is indicated in the Figure; for example, it was more for section *A* than *B*. At the level of section *C*, once the inferior occipital sulcus had become deeper, it was necessary to reverse the drawings of the contours of the sections (as shown in *C*) to prevent the two sets of contour lines – one for the lunate and the other for the inferior occipital sulcus – from crossing over. The representative sections *A–D* were taken at levels indicated on the surface drawing of the brain to the lower left. In the centre, the detailed reconstruction shows the continuity of the degeneration from the anterior bank of the lunate sulcus to the posterior lip of the inferior occipital sulcus. Conventions as in previous figures. The degeneration in the posterior bank of the superior temporal sulcus is not shown in this Figure, nor are the differences in the calibre of the degenerating fibres indicated. The dots on the lines in the central reconstruction indicate degeneration.



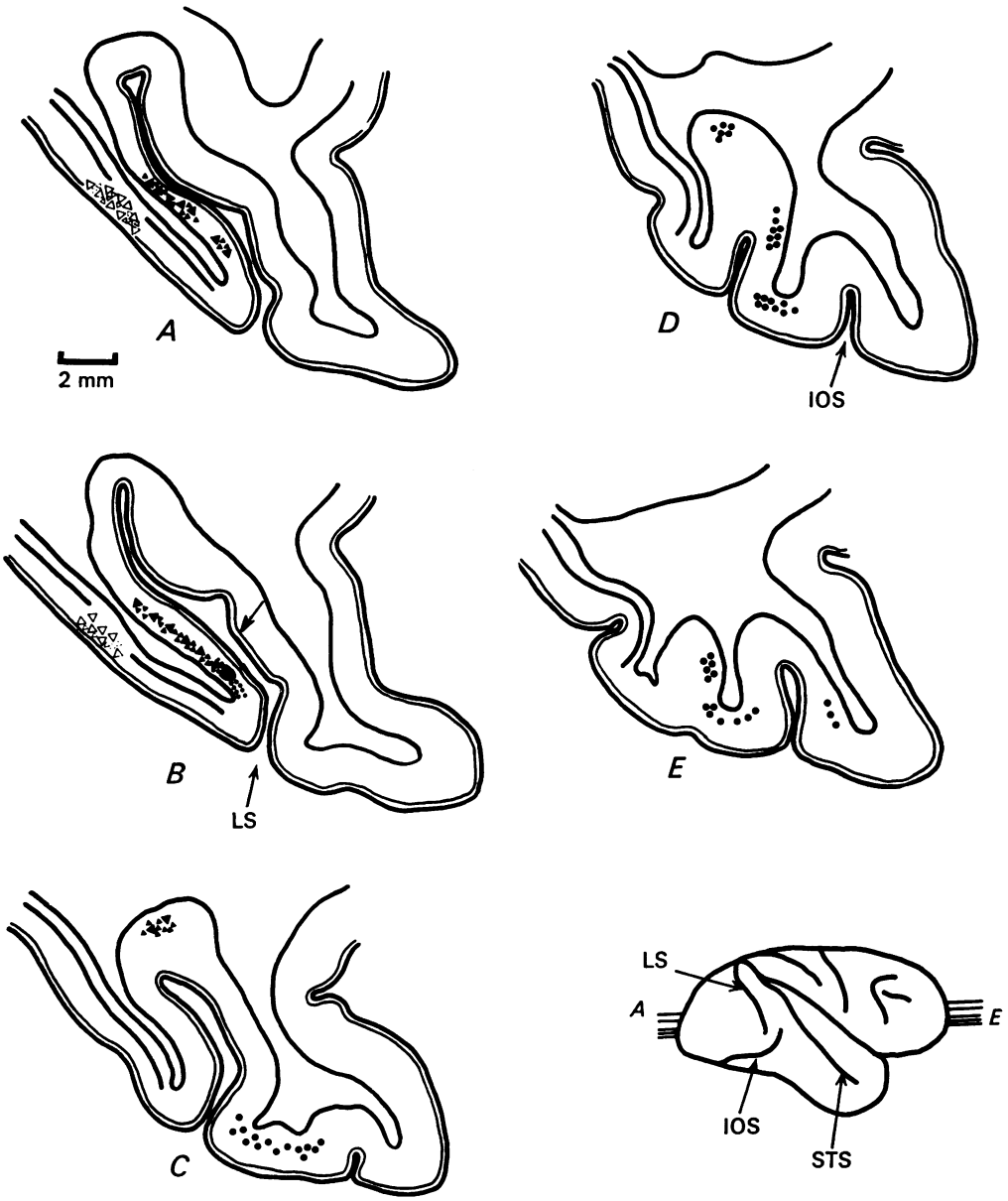
Text-fig. 6. Reconstruction of a double-label anatomical experiment in which a lesion was made in foveal striate cortex and [^{3}H]proline was injected into non-foveal striate cortex of the same hemisphere. The site of injection is shown by open triangles and the label distribution by filled triangles. Conventions as in previous Figures. Note the presence of degeneration (due to the lesion) in the anterior bank of the lunate sulcus in sections *C–G* and in the posterior lip of the inferior occipital sulcus in section *F*. Note also the absence of label in these regions. The label, due to the injection into a non-foveal region of V1, is distributed more medially within the inferior occipital sulcus.

areas in the anterior bank of the lunate sulcus, but this has been rare enough to suggest that direct projections from non-foveal striate cortex to the fourth visual areas are either non-existent or very sparse.

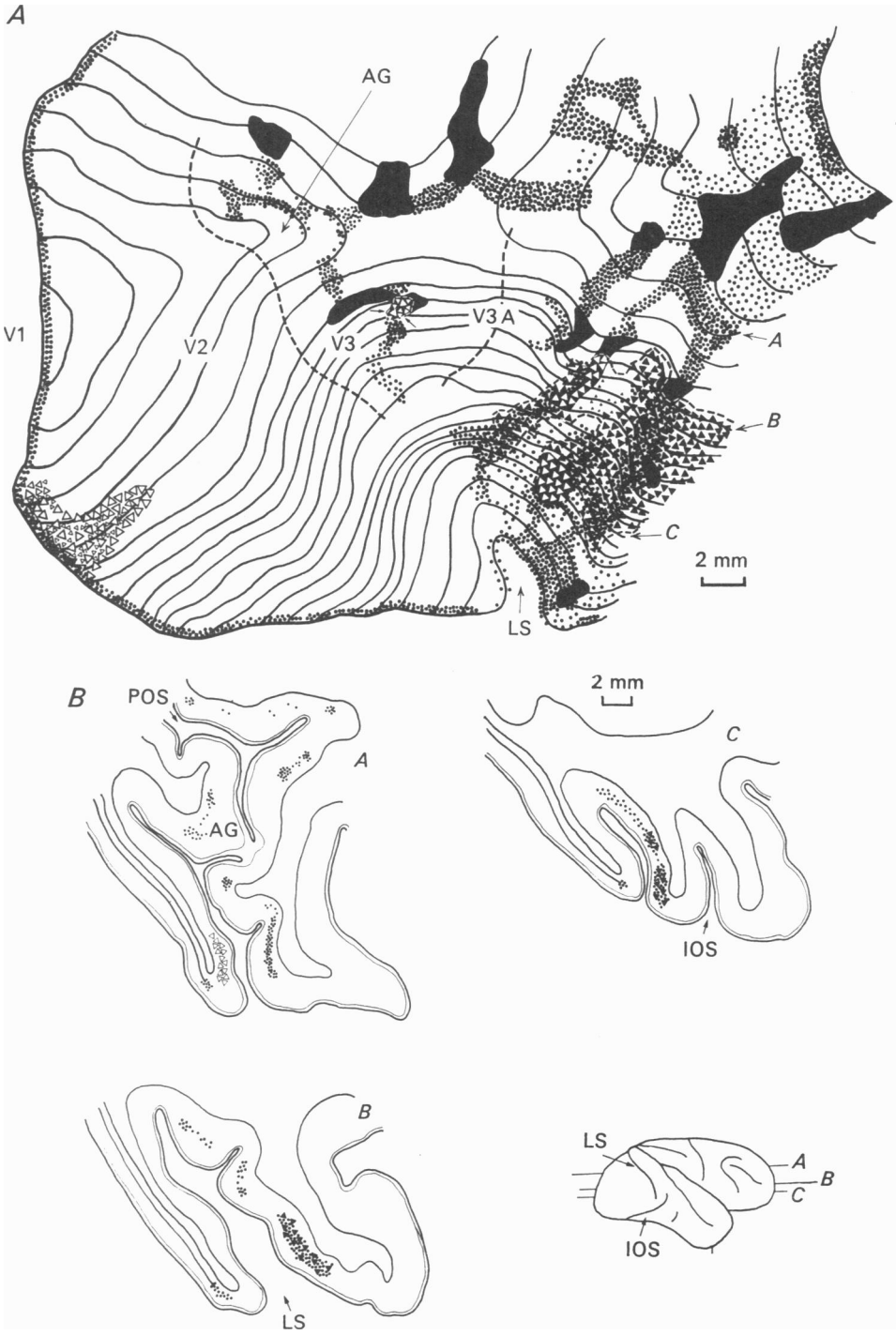
Perhaps a more convincing way of showing this difference in the projections of the foveal and extrafoveal parts of the striate cortex is to use a double labelling procedure in the same hemisphere, as has already been done in studying other aspects of the organization of the prestriate cortex (Zeki, 1976, 1977*a*). In such an approach, a lesion can be made in the region of foveal representation of the striate cortex and radioactive label injected into a non-foveal representation region of area 17 of the same hemisphere. The distribution of the degeneration following a foveal lesion and of the label following an extrafoveal injection can then be directly compared in the same hemisphere to see whether there is any dissociation in the projections of the foveal and non-foveal parts of V1. Such an experiment is illustrated in Text-fig. 6. In this animal, the label was injected into that part of the striate cortex in which the visual fields at about 2° above the centre of gaze are represented whereas the lesion was made in that part of V1 in which the centre of gaze is represented. It can be seen that the degeneration (shown as dots) following the lesion in the foveal part of V1 extends to the anterior bank of the lunate sulcus and continues ventrally to the posterior lip of the inferior occipital sulcus. The label (shown as filled triangles), by contrast, is distributed more medially within the inferior occipital sulcus and does not appear anywhere within the region which, on anatomical and physiological grounds, is regarded as part of the fourth visual areas.

In an earlier study (Zeki, 1971), it was shown that the fourth visual areas receive a direct input from V2. Indeed, they were originally defined on that basis. So far all the parts of V2 in which central visual fields are represented have been found to project to V4. As described above, this is not true of V1, since only the foveal region of V1 sends a direct input to V4 whereas non-foveal regions do not. However, all parts of V1 project to V2 (Cragg, 1969; Zeki, 1969). The consequences of this are that those regions of V2 which receive from non-foveal regions of V1 project directly to V4, whereas the corresponding parts of V1 do not. Text-fig. 7 shows this directly in another experiment using double tracers. In this experiment, [^{3}H]proline was injected into a non-foveal region of V1 and a lesion was made in that part of V2 to which the injected part of V1 projects. The aim was to show that, unlike foveal V1, non-foveal V1 does not project directly to V4, but only through V2. As before, the distribution of label is shown as filled triangles and of degeneration as dots. Note (*a*) that label, following an injection into a non-foveal part of V1, is distributed within that part of V2 in which the lesion was made; (*b*) that there is no label in the anterior bank of the lunate sulcus (V4); and consequently, no direct projections from non-foveal V1 to V4; (*c*) that there is, by contrast, degeneration in V4 due to the lesion in that part of V2 receiving a projection from a non-foveal part of V1 which, itself, does not project to V4. Consequently, such an experiment shows that the projections from non-foveal parts of V1 to V4 are not direct, but through V2.

Although such experiments demonstrate that foveal striate cortex projects directly to a part of the fourth visual complex, contrasting with the non-foveal parts of V1, which do not project directly to V4, but only through V2, it is evident at a glance from Text-figs. 3–5 that the projections from foveal striate cortex are only to a small



Text-fig. 7. Reconstruction of a double-label anatomical experiment in which [^{3}H]proline was injected into a region of V1 representing the lower visual fields at about 2–3° from the centre of gaze. The site of the injection is shown by open triangles and the distribution of label due to this injection is shown as filled triangles. In the same hemisphere, a small electrolytic lesion (shown in solid black and indicated by an arrow) was made in that region of V2 in which there was label distribution following an injection into a non-foveal part of V1. Note (*a*) the presence of degeneration (due to the lesion) in the anterior bank of the lunate sulcus, the surface of the prelunate gyrus, as well as in the anterior bank of the parieto-occipital sulcus, and (*b*) the absence of label in these areas. This experiment shows that non-foveal parts of V1 do not project directly to V4, but only through V2.



Text-fig. 8. For legend see facing page.

part of V4, since degeneration following a foveal striate lesion appears in the anterior bank of the lunate sulcus only when this sulcus has become shallow. Even though the callosal bands that define V4 extend dorsally in the lunate sulcus and the prelunate gyrus (Zeki, 1970; Van Essen & Zeki, 1978), the exact dorsal and ventral boundaries of V4 itself are still not clear. Nevertheless, it is quite clear that the fourth visual complex is a more extensive area than the part that receives a direct input from foveal striate cortex and can be followed superiorly in the anterior bank of the lunate sulcus to regions to which there does not appear to be a direct projection from foveal striate cortex, although these same regions do receive an input from V2. Despite the uncertain upper limits of V4, one can nevertheless compare the *extent* of the projections to V4 from foveal striate cortex and from V2 by injecting radioactive label into either one of these regions in animals in which the splenium of the corpus callosum had been sectioned and note how far dorsally the label distributes in either case, in relation to the bands of callosal degeneration. Text-fig. 8*A*, *B* illustrates an experiment in which radioactive label was injected into the region of vertical meridian representation in V2 in an animal in which the splenium of the corpus callosum had been sectioned 6 days before the injection. The site of label injection is indicated by open triangles, the degeneration is represented as dots, or, where very heavy, is shown in black. Label distribution is shown as filled triangles. It can be seen that there is heavy distribution of label, in two major patches, in the anterior bank of the lunate sulcus in the regions of the callosal bands that define V4 (Zeki, 1970; Van Essen & Zeki, 1978). But note that the label distribution terminates abruptly at the level at which the annectant gyrus appears. Even though the bands of callosal degeneration that define V4 continue dorsally beyond this level, it is not clear whether V4 itself does. Certainly I have not, so far, observed projections to the anterior bank of the lunate sulcus from central V2 at levels dorsal to the appearance of the annectant gyrus (S. M. Zeki, unpublished results). Note that label also appears in the region of the

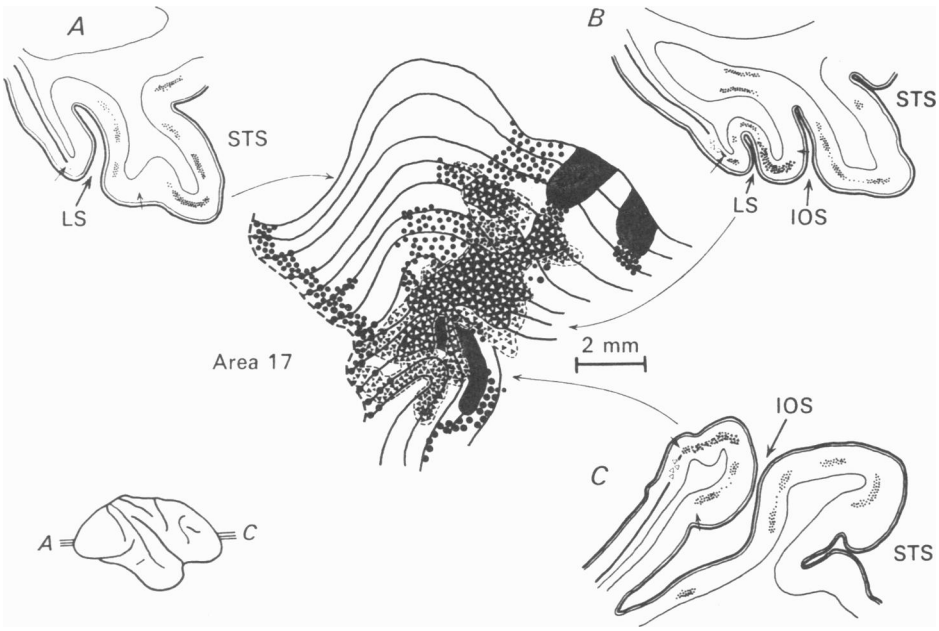
---

Text-fig. 8. *A*, a reconstruction of an anatomical experiment in which [^{3}H]proline was injected into the region of vertical meridian representation of V2 in the posterior bank of the lunate sulcus (see Text-fig. 8*B*) in an animal whose corpus callosum had been sectioned 6 days before the injection. Conventions as in previous figures in which double label anatomical experiments are reconstructed. In this Figure, much of the prestriate cortex has been reconstructed, as described elsewhere (Van Essen & Zeki, 1978) but the lunate sulcus is reconstructed in greater detail (at closer intervals). Areas of heavy degeneration are shown in black. Areas of moderate or sparse degeneration are indicated by the frequency of the solid circles. Regions of label distribution are indicated by filled triangles and are enclosed by dashed lines. Note the heavy distribution of label in the anterior bank of the lunate sulcus, in two major patches. The label falls in the region of the patches of callosal degenerating defining V4. Although this zone of callosal degeneration continues superiorly along the prelunate gyrus, no label is found anywhere within this zone dorsal to the level of the annectant gyrus (AG). Note also the distribution of label within the zone of callosal degeneration defining the anterior border of V3 (arrows). Dashed lines indicate the regions of horizontal meridian representation at the V2–V3 boundary and within V3A. See also Text-fig. 8*B*.

B, tracings through representative horizontal sections of the same brain as the one reconstructed in Text–fig. 8*A* to show the distribution of the label and the callosal degeneration. The figures correspond to their homologues in Text-fig. 8*A*. Conventions as in previous Figures.

callosal band defining the anterior boundary of V3, confirming earlier anatomical results (Zeki, 1971).

If one were to compare this pattern of projections from V2 to V4 with that from foveal striate cortex to V4 (Text-fig. 9), the more limited extent of the projections from the latter to V4 become immediately apparent. The experiment illustrated in Text-fig. 9 was identical to that of Text-fig. 8, except that the label was injected into foveal striate cortex. The conventions in the two figures are similar, except that in



Text-fig. 9. Reconstruction of a double label anatomical experiment in which [^{3}H]proline was injected into foveal striate cortex in an animal whose corpus callosum had been sectioned six days before the injection. Conventions as in Text-fig. 8. Representative sections to show the injection site, the distribution of label and of degeneration at the levels indicated on the drawing of the brain to the lower left, are shown. In this brain only the lower part of the lunate sulcus and the posterior lip of the inferior occipital sulcus have been reconstructed since label appeared in the lunate sulcus only when this sulcus had become very shallow. The band of degeneration defining the anterior border of V3 has disappeared (but see Zeki, 1978*b*). The label appears within the band of degeneration defining V4 and is continuous to the posterior lip of the inferior occipital sulcus. The band of callosal degeneration defining V4 continues dorsally but label was not found within this dorsal continuation.

Text-fig. 9 only the anterior bank of the lunate sulcus has been reconstructed. The callosal degeneration defining the fourth visual complex continues dorsally to the level at which the annectant gyrus appears, and beyond, but there was no label anywhere within this region. Instead the label only appeared at a level at which the lunate sulcus had become very shallow and continued down to the posterior lip of the inferior occipital sulcus.

These experiments show, therefore, that foveal striate cortex projects to a limited part of V4 only. They also show that, by contrast, V2 sends a more extensive input to

V4 which includes those limited parts of V4 that receive a direct input from foveal striate cortex (Zeki, 1971*a*). The clear implication is that these limited parts of V4 receive a double input, one from foveal striate cortex and another one from V2.

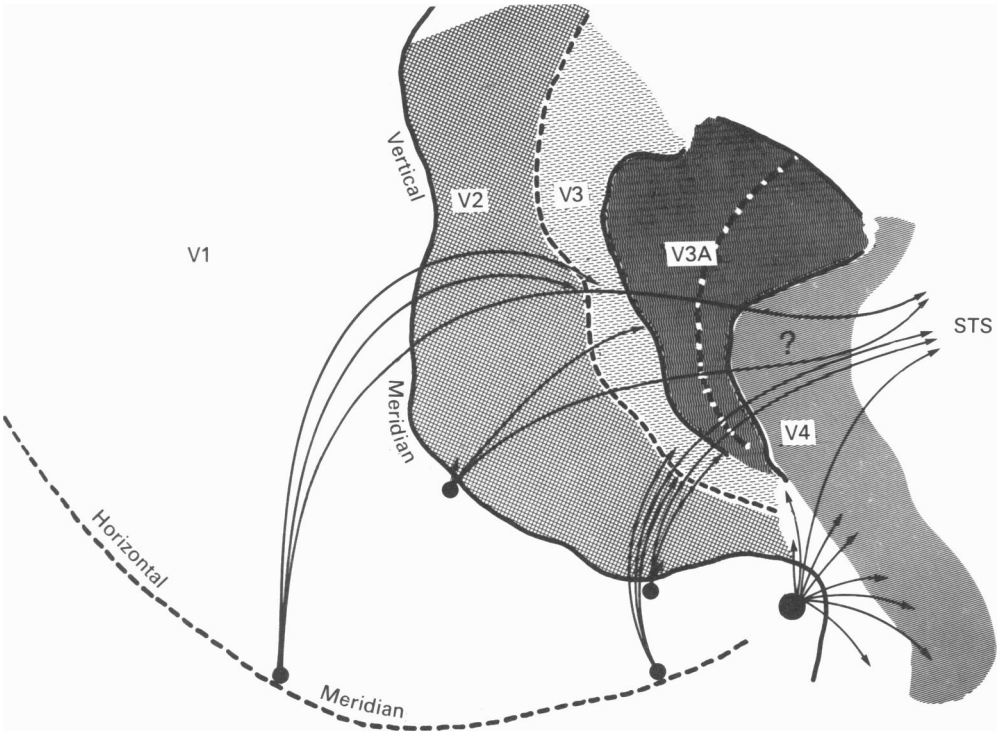
DISCUSSION

In the rhesus monkey, the retina projects, in a topographical manner, to the striate cortex through the lateral geniculate nucleus. Since the cortical projection of the lateral geniculate nucleus in this species is exclusively to the striate cortex (Wilson & Cragg, 1967), all the information contained in this pathway, even that destined to be analysed in the visual areas of the prestriate cortex, is relayed to it. The way that the striate cortex deals with the topographically organized information reaching it from the retina is simply to allot relatively more cortical space to the rod-free area of the retina, in an otherwise topographic map of the visual field (Daniel & Whitteridge, 1961; Guld & Bertulis, 1976). One consequence, among others, of such an arrangement is the concentration of visual information relating to colour in the region of foveolar representation, compared to regions of more peripheral representation (Hubel & Wiesel, 1968; Dow & Gouras, 1973; Gouras, 1974), since the cones are themselves concentrated in the fovea.

In its outward projections, to the prestriate cortex, the striate cortex appears to use two different strategies, both of them traceable to the topographic representation of the visual fields within it. One strategy consists of separating out the different types of information, *relating to the same part of the visual fields*, and distributing these to different prestriate areas. This is evident from the summary diagram of the projections of striate cortex, based on the work reported here, as well as antecedent results (Cragg, 1969; Zeki, 1969, 1971*a*,*b* 1977*a*) (Text-fig. 10). This Figure shows that every part of the striate cortex projects to V2, V3 and the visual area in the medial part of the posterior bank of the superior temporal sulcus (although it is more difficult to be certain whether foveal striate cortex projects to V3 – see Zeki, 1978*a*). These are well defined areas of the prestriate cortex which appear to differ from one another functionally (Zeki, 1975; 1978*b*). Given the functional differences between the areas to which V1 projects, it would be difficult to imagine that the information sent out to them from the striate cortex is the same information. Indeed, the very differences in the anatomy of the projections from the striate cortex to these three prestriate areas hints strongly that there must be differences in the type of information sent to them. For example, the degeneration in V2 following a lesion on the lateral surface of V1 is not only more extensive, but also finer than the degeneration in V3 or in the posterior bank of the superior temporal sulcus.

Another strategy, also evident in Text-fig. 10, which the striate cortex uses in distributing information to the visual areas of the prestriate cortex is to *differentiate, in its projections, between the representation of different parts of the retina.* That the striate cortex almost certainly uses this strategy as well, is evident from the results of this study which have shown that the very region of the striate cortex containing the highest concentration of colour-coded cells projects not only to those areas of the prestriate cortex which other parts of the striate cortex project to, but has an additional projection – to V4, precisely that part of the prestriate cortex in which there is

a heavy concentration of colour coded cells (Zeki, 1973, 1975). It is remarkable that even if a lesion were to be made in a region of the striate cortex representing no more than 2° from the centre of gaze, one observes, at best, only a few degenerating fibres in the cortex of V4, and often none at all. Rather than the simple scaling difference between centre and periphery that one might expect, the difference in the projection of foveal and non-foveal striate cortex appears to be a good deal sharper.



Text-fig. 10. Summary diagram of the projections of the striate cortex, based on information obtained in this and previous studies. Interrupted lines indicate the representation of the horizontal meridian, continuous lines that of the vertical meridian. The gap between the STS region and the other prestriate areas depicted here refers to the surface of the prelunate gyrus and the lateral part of the posterior bank of the superior temporal sulcus (STS). Only the projections of the part of the striate cortex representing lower visual fields are shown.

I do not wish to imply that the properties of the colour coded cells in V4 are explicable solely by an input from foveal striate cortex. Indeed, the reverse is the case, given the larger receptive field sizes of cells in V4. It is known that V2, containing something in the region of 8 % colour-coded cells, larger in receptive field size than those in V1 (Zeki, 1978*b*) as well as the pulvinar (Cragg, 1969; Benevento & Rezak, 1976) both project to V4 and may well play a role in generating the properties of the cells there. As well, foveal striate cortex does not project to the whole of V4 but only to limited regions within it. There are, on the other hand, complicated sets of interconnexions within V4 (Zeki, 1971*a*, 1977*b*). All this argues against a simple system which would seek to explain the properties of the colour-coded cells in V4 solely by an

input from foveal striate cortex. The aim in the present paper has been simply to show that the part of the prestriate cortex in which there is a heavy concentration of colour-coded cells receives a direct input from the part of the striate cortex in which colour coded cells are most heavily concentrated. When this evidence is considered against the background of other anatomical evidence which shows that both foveal and non-foveal striate cortex project to other anatomically well defined prestriate areas which are poor or absent in colour-coded cells, but which have other specific properties (Zeki, 1978*b*), it becomes compelling enough to suggest that another function of the striate cortex must be to segregate out the different types of information coming from the eyes and to parcel this information out to different prestriate visual areas for further analysis.

Why all the information in the retino-geniculo-cortical pathways passes through the striate cortex and the extent to which the striate cortex modifies or rearranges the information it receives before parcelling it out, remains for future studies to determine.

This work was supported by the Science Research Council.

I am greatly indebted to Ms Brenda Crane and Ms Pamela Jacobs for their excellent histological assistance.

It is a pleasure to thank Professor Mathew Alpern and Professor J. Z. Young for their critical reading of this manuscript.

REFERENCES

BENEVENTO, L. A. & REZAK, M. (1976). The cortical projections of the inferior pulvinar and adjacent lateral pulvinar in the rhesus monkey (*Macaca mulatta*) an autoradiographic study. *Brain Res.* **108**, 1–24.

BOYCOTT, B. & DOWLING, J. E. (1969). Organisation of the primate retina: Light microscopy. *Phil. Trans. R. Soc.* B **255**, 109–184.

COWAN, W. M., GOTTLIEB, D. I., PRICE, J. L. & WOOLSEY, T. A. (1972). The autoradiographic demonstration of axonal connections in the central nervous system. *Brain Res.* **37**, 21–51.

CRAGG, B. G. (1969). The topography of the afferent projections in the circumstriate visual cortex of the monkey studied by the Nauta method. *Vision Res.* **9**, 733–747.

DANIEL, P. M. & WHITTERIDGE, D. (1961). The representation of the visual field on the cerebral cortex in monkeys. *J. Physiol.* **159**, 203–221.

DOW, B. M. & GOURAS, P. (1973). Color and spatial specificity of single units in rhesus monkey foveal striate cortex. *J. Neurophysiol.* **36**, 79–100.

GOURAS, P. (1974). Opponent colour cells in different layers of foveal striate cortex. *J. Physiol.* **238**, 583–602.

GULD, C. & BERTULIS, A. (1976). Representation of fovea in the striate cortex of vervet monkey, *Cercopithecus aethiops pygerythrus*. *Vision Res.* **16**, 629–631.

HUBEL, D. H. & WIESEL, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *J. Physiol.* **195**, 215–243.

HUBEL, D. H. & WIESEL, T. N. (1974). Uniformity of monkey striate cortex: a parallel relationship between field size, scatter and magnification factor. *J. comp. Neurol.* **158**, 295–306.

ØSTERBERG, G. (1935). Topography of the layer of rods and cones in the human retina. *Acta ophthal.* Suppl. 6.

TALBOT, S. A. & MARSHALL, W. H. (1941). Physiological studies on neural mechanism of visual localization and discrimination. *Am. J. Ophthal.* **24**, 1255–1264.

VAN BUREN, J. M. (1963). *The Retinal Ganglian Cell Layer*. Springfield, Ill.: Charles C. Thomas.

VAN ESSEN, D. & ZEKI, S. (1978). The topographic organisation of rhesus monkey prestriate cortex. *J. Physiol.* **277**, 193–226.

WILSON, M. E. & CRAGG, B. G. (1967). Projections from the lateral geniculate nucleus in the cat and monkey. *J. Anat.* **101**, 677–692.

WITTANEN, J. T. (1969). Selective silver impregnation of degenerating axons and axon terminals in the central nervous system of the monkey (*Macaca mulatta*). *Brain Res.* **14**, 546–548.

ZEKI, S. M. (1969). Representation of central visual fields in prestriate cortex of monkey. *Brain Res.* **14**, 271–291.

ZEKI, S. M. (1970). Interhemispheric connections of prestriate cortex in monkey. *Brain Res.* **19**, 63–75.

ZEKI, S. M. (1971*a*). Cortical projections from two prestriate areas in the monkey. *Brain Res.* **34**, 19–35.

ZEKI, S. M. (1971*b*). Convergent input from the striate cortex (area 17) to the cortex of the superior temporal sulcus in the rhesus monkey. *Brain Res.* **28**, 338–340.

ZEKI, S. M. (1973). Colour coding in rhesus monkey prestriate cortex. *Brain Res.* **53**, 422–427.

ZEKI, S. M. (1975). The functional organization of projections from striate to prestriate visual cortex in the rhesus monkey. *Cold Spring Harb. Symp. quant. Biol.* **40**, 591–600.

ZEKI, S. M. (1976). The projections to the superior temporal sulcus from areas 17 and 18 in the rhesus monkey. *Proc. R. Soc.* B **193**, 199–207.

ZEKI, S. M. (1977*a*). Simultaneous anatomical demonstration of the representation of the vertical and horizontal meridians in areas V2 and V3 of rhesus monkey visual cortex. *Proc. R. Soc.* B **195**, 517–523.

ZEKI, S. M. (1977*b*). Colour coding in the superior temporal sulcus of rhesus monkey visual cortex. *Proc. R. Soc.* B **197**, 195–223.

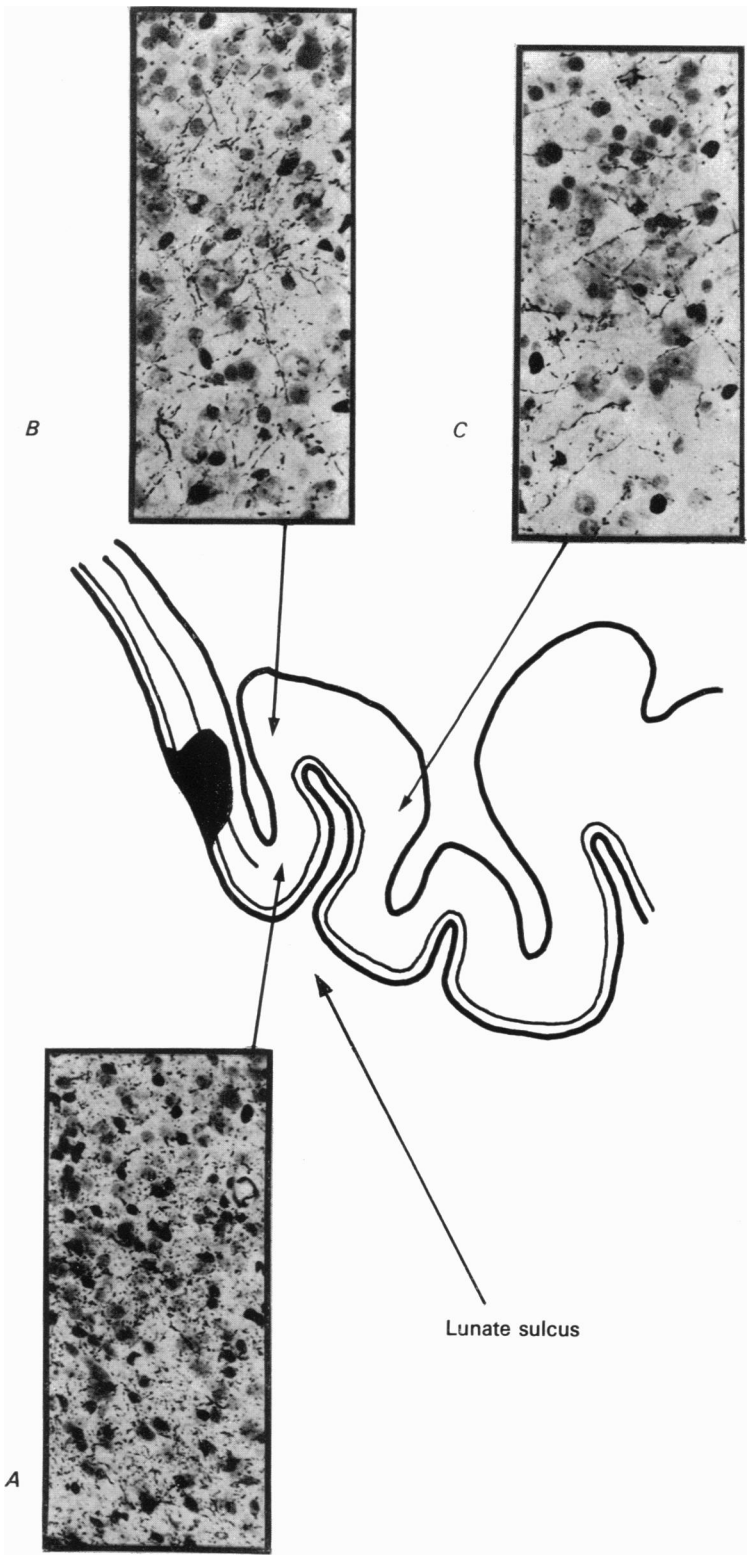
ZEKI, S. M. (1978*a*). The third visual complex of rhesus monkey prestriate cortex. *J. Physiol.* **277**, 245–272.

ZEKI, S. M. (1978*b*). Uniformity and diversity of structure and function in rhesus monkey prestriate visual cortex. *J. Physiol.* **277**, 273–290.

ZEKI, S. M. & SANDEMAN, D. R. (1976). Combined anatomical and electrophysiological studies on the boundary between the second and third visual areas of rhesus monkey cortex. *Proc. R. Soc.* B **194**, 555–562.

EXPLANATION OF PLATE

The degeneration in different parts of the lunate sulcus, following a foveal striate cortex lesion. The lesion is shown in solid black in the central tracing of a horizontal section. *A*, the degeneration in the posterior bank of the lunate sulcus (V2); *B*, in its depth; *C*, in the anterior bank of the lunate sulcus (V4). Note that the degeneration in *A* is fine and dense compared to that in *B*. The degeneration is sparsest in *C*, at this level, but increases in density at more ventral levels. The question of whether the degeneration in *B* corresponds to V3 is discussed in the text and in a companion paper (Zeki, 1978*a*). × 400.



(*Facing p.* 244)