A direct projection from area V1 to area V3A of rhesus monkey visual cortex

By S. Zeki

Department of Anatomy, University College London, Gower Street, London WC1E 6BT, U.K.

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Small cortical lesions were made in regions of the primary visual cortex (V1) representing different retinal eccentricities. It was found that, whereas all parts of V1 project to visual areas V2, V3 and the motion area of the superior temporal sulcus, only parts of V1 representing peripheral eccentricities (in excess of 30°) project directly to visual area V3A.

Introduction

The visual cortex of the rhesus monkey consists of a multiplicity of distinct areas (see Zeki (1978a) for a review). Chief among these is the primary visual cortex (V1). It receives all the fibres in the retino–geniculo-cortical pathways (Wilson & Cragg 1967). Hence all the information transmitted by this pathway, even that destined ultimately for other visual areas, passes through V1. Area V1, in turn, sends direct and independent projections to other visual areas, situated in a broad zone of cortex known as the prestriate cortex (Zeki 1978b). It would be difficult to suppose that the same information is sent in these independent pathways to the different, functionally specialized, visual areas of the prestriate cortex (Zeki 1978a, b). It would be more logical to conclude that V1, in addition to its other visual functions (Hubel & Wiesel 1977), acts as a distribution centre, sending different types of information to different visual areas (Zeki 1976, 1978b). The evidence for such a supposition comes partly from electrophysiological recording experiments, which have shown that the different visual areas to which V1 projects differ in their functional properties (Zeki 1978a, c). It also comes, in part, from anatomical studies. These have shown that the topographic arrangement and fibre diameter of the projections to the different areas are themselves different (Zeki 1969, 1971, 1977a; Cragg 1969). Moreover, they show that the presence and density of projections from V1 to the visual areas of the prestriate cortex may be dictated by the retinal representation in V1. Thus, whereas all parts of V1 studied have been shown to project to V2, V3 and the motion area of the superior temporal sulcus (Zeki 1969, 1971; Cragg 1969), parts of V1 in which the central 10° of the retina are represented send a less powerful input to V3 than
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do regions of V1 in which more peripheral parts of the retina are represented (Zeki 1977a, 1978d). Moreover, only the region of foveolar representation in V1 sends a direct projection to V4 (Zeki 1978b).

In the present paper, further anatomical evidence is given to show that regions of V1 in which different retinal eccentricities are represented may also differ in their cortical projections.

Materials and methods

Five rhesus monkeys were used in the present study. In three, small cortical lesions were made in V1, and the animals were sacrificed nine days postoperatively. In the other two, the splenium of the corpus callosum was sectioned and the animals were allowed to survive 6 days. Two days before sacrifice, a mixture of [3H]proline and [3H]fucose was injected into V1. All operations were performed under Nembutal anaesthesia. Details of surgical and histological procedures are given elsewhere (Zeki 1969, 1970, 1977a).

In addition to the above, numerous brains from preceding experiments were available for study.

Results

Figure 1 is a diagrammatic reconstruction of an anatomical experiment in which a small cortical lesion was made in V1. The lesion was situated in a part of V1 representing a retinal position about 3° from the centre of gaze below the horizontal meridian (Daniel & Whitteridge 1962). Three patches of fibre degeneration appeared. One, consisting of fine fibres, was situated in the posterior bank of the inferior occipital sulcus. A second, consisting of coarse fibres, was in the anterior bank of the same sulcus. A third area of degeneration was situated in the posterior bank of the superior temporal sulcus (see also Zeki 1969; Cragg 1969). If a similar-sized lesion is made on the dorsolateral surface of V1 (representing the upper part of the retina) the first two patches of degeneration (belonging to areas V2 and V3, respectively) would appear in the lunate sulcus. The third patch would appear in much the same position of the posterior bank of the superior temporal sulcus (Zeki 1969, 1971; Cragg 1969). With neither lesion would degeneration appear in any other area of the prestriate cortex beyond the ones described above.

Figure 2 is a diagrammatic reconstruction of another anatomical experiment, in which a more extensive lesion was made in V1. Starting on the lateral surface where the central 10° of the retina are represented, a small lesion was made by subpial aspiration and then the pipette was pushed in further to make another small lesion, in the posterior bank of the upper trunk of the calcarine sulcus. Here the retina at about 15–20° from the centre of gaze is represented (Zeki, unpublished results). Five areas of degeneration appeared. Of these, two were
in the lunate sulcus, a fine one belonging to V2 and a coarse one belonging to V3; two were in the parieto-occipital sulcus, a fine one belonging to the peripheral extension of V2 and a coarse one belonging to the peripheral extension of V3 (Zeki 1977a). Finally, degeneration also appeared in the posterior bank of the

**Figure 1.** Diagrammatic reconstruction of an anatomical experiment in which a lesion was made in V1, at the position shown (in black) on the surface drawing of the brain. The degeneration resulting in the prestriped cortex is shown in representative sections, taken at the levels indicated. The degeneration is shown as small or large dots, depending upon the calibre of the degenerating fibres. Continuous line in cortex indicates striate cortex. Abbreviations: l.s., lunate sulcus; i.o.s., inferior occipital sulcus; s.t.s., superior temporal sulcus; c.s., calcarine sulcus; p.o.s., parieto-occipital sulcus.

superior temporal sulcus. Confirming our previous conclusions (Zeki 1978c), there was no degeneration in area V3A, either in the portion lying in the lunate sulcus or in that lying in the parieto-occipital sulcus.

In the experiment reconstructed in figure 3, the lesion in V1 was more extensive still. Using the same approach described above, I made the first two lesions as in the previous monkey, although the position of entry of the pipette was somewhat more ventral than in the previous animal. Following the second lesion, the pipette was pushed deeper still and a third lesion was made in the ventral bank of the calcarine sulcus, which represents retinal eccentricities in excess of 40°
(Zeki, unpublished results). As might be expected from such widespread, but discontinuous, lesions in V1, the degeneration in the prestriate cortex was extensive. Much of the degeneration still appeared in various parts of V2 and V3 and in the posterior bank of the superior temporal sulcus. But in this instance degenerating fibres also appeared in area V3A.

![Diagram](image)

**Figure 2.** Diagrammatic reconstruction of an anatomical experiment in which a lesion was made on the lateral surface and another one in the depth of the upper trunk of the calcarine sulcus. Conventions as in figure 1.

As expected, there was degeneration in both the lunate and inferior occipital sulci (see above) as well as in the posterior bank of the superior temporal sulcus. Degeneration also appeared in the parieto-occipital sulcus (compare with figure 2), where the more peripheral portions of V2 and V3 are represented. But there was another, more anterior, field of degeneration (marked with an arrow in figure 3, A–B) in the parieto-occipital sulcus, which was almost certainly within visual area V3A. In addition to the above, degeneration also appeared in the medial part of the anterior bank of the occipito-temporal sulcus. This latter patch of degeneration was complex, often breaking up into several patches of dense degeneration, bridged across by regions of sparse degeneration.

Area V3A is a visual area extending from the anterior bank of the lunate sulcus, across the annectant gyrus and into the parieto-occipital sulcus. It lies anterior to visual area V3 (Zeki 1978d; van Essen & Zeki 1978). Its boundaries, as well as those of other visual areas, are often best, and most easily, defined by using the callosal connections of the prestriate cortex as a guide, since each area has its own, independent callosal connections (Zeki 1976, 1977b; Zeki & Sandeman 1976). It therefore seemed worth while to repeat this experiment with a combination of anatomical techniques (Zeki 1977a, b), to ensure that more peripheral parts of V1
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**Figure 3.** Diagrammatic reconstruction of an anatomical experiment in which a lesion was made at three different regions in striate cortex. Conventions as in previous figures; o.t.s., occipito-temporal sulcus.
Figure 4. Diagrammatic reconstruction of an anatomical experiment in which the splenium of the corpus callosum was sectioned and labelled amino acids were injected into V1. Site of label injection is shown in black; label distribution is shown as triangles. Degeneration is depicted as dots. Conventions as in previous figures.
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do indeed project directly to V3A. Accordingly, in a two-stage experiment (reconstructed in figure 4), the splenium of the corpus callosum was first sectioned. The degeneration resulting from such a procedure would define the boundaries of the visual areas, including those of V3A. Two days before sacrifice, labelled amino acids were injected into regions of V1 closely similar to the positions where lesions had been made in the previous animal (see figure 3). The labelled amino acids would be taken up by the nerve cells and transported to their axon terminals, thus showing to where the injected regions project. The results are shown in figure 4. The distribution of the label (shown as triangles) is identical to the distribution of the degeneration in figure 3 and requires no further description. But the presence of the callosal degeneration allows one to place the label in the depth of the parieto-occipital sulcus (marked with an arrow) as being unambiguously in area V3A.

We also note that there was an area of heavy label in the occipito-temporal sulcus, confirming the results shown in figure 3.

Discussion

The experiments reported in this paper are an extension of our previous studies on the projections of the primary visual cortex (Zeki 1969, 1977a, 1978a, b, d; Cragg 1969). In these earlier studies, we showed that regions of V1 subserving the central 30° of the retina send direct and independent projections to areas V2 and V3, and another, highly convergent one, to the motion area of the superior temporal sulcus (Zeki 1971). Furthermore, direct projections from V1 to the fourth visual areas (V4) are absent except from the region of foveolar representation in V1 (Zeki 1978a, b). In the present study, it has been shown that there are no direct projections from parts of V1 subserving the central 20–30° of the retina to area V3A. By contrast, such direct projections do exist from regions of V1 representing retinal eccentricities in excess of 30°.

This demonstration supports the view that, in distributing information from V1 to the visual areas of the prestriate cortex, two strategies are used (Zeki 1978a, b). Of these, one is to distribute different types of information, relating to the same retinal position, to different visual areas. The other is to distinguish between different retinal positions in organizing these projections.

It is, of course, difficult to understand why central parts of V1 do not project to V3A while more peripheral parts do. In the instance of a direct projection from foveolar striate cortex to V4, the reasons are perhaps easier to understand. V4 is an area rich in colour-coded cells (Zeki 1978a) and it makes sense that it should receive a direct input from that region of V1 representing the rod-free area of the retina. No ready explanation is available for the pattern of projections from V1 to V3A. Such an explanation must await a more detailed study of the functional properties of cells in V3A.
Finally, it is likely that the observed projection to the occipito-temporal sulcus is to very peripheral parts of V2 and V3. But, not having traced V2 and V3 directly to that position, we are not sure that this is so. To ascertain this, a more detailed anatomical study would be required and, until this is done, we would not wish to commit ourselves.

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References

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