

**CELLS RESPONDING TO
CHANGING IMAGE SIZE AND DISPARITY IN THE
CORTEX OF THE RHESUS MONKEY**

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SUMMARY

1. The cells of the cortex of the posterior bank of the superior temporal sulcus of the monkey appear to be specialized to signal motion in the visual field. In this paper, cells in this cortical area capable of signalling motion towards or away from the animal are described.

2. Two such types of cell were encountered. One type, the opposed movement complex and opposed movement hypercomplex cells, responded to two edges at a given orientation moving towards or away from each other within the receptive fields. These cells were driven either monocularly or binocularly, but when binocularly driven the cells responded in an identical manner to stimulation of each eye, thus suggesting that such cells must receive a double, and opposed, input from each eye. The other type of cell, always binocularly driven, responded to movement in opposite directions on the two retinas, thus suggesting that such cells must receive diametrically opposite connexions from the two eyes.

3. Long penetrations made to study the manner in which such cells were grouped together in the cortex revealed that they were arranged in small groups or clusters, separated from each other by the common directionally selective cells so prominently present in this area. Thus, cells with one type of wiring mechanism were separated from each other by cells receiving another, and more common, type of anatomical wiring.

INTRODUCTION

The cells of the cortex of the posterior bank of the superior temporal sulcus in the rhesus monkey appear to be specialized to detect motion. Some cells respond to motion of any contour within their receptive field and others respond optimally to motion of specific contours. The great majority of both types of cell are directionally selective (Dubner & Zeki,

1971; Zeki, 1974). Although preferences for one eye or the other are common, the cells are usually binocularly driven and receptive field position and properties are the same for the two eyes, thus suggesting that such cells have anatomically identical sets of connexions with each eye, although for some cells the set of connexions from one eye may be more powerful in driving the cell than that from the other eye.

However, for cells to signal motion towards or away from the animal, with the resultant changing disparity, a more complicated set of neural connexions would be required. Such cells must be wired in diametrically opposed ways to the two eyes or have diametrically opposed connexions with each eye. Although rare, cells using these two different wiring mechanisms to signal centripetal and centrifugal motion do exist in the cortex of the posterior bank of the superior temporal sulcus and are of sufficient interest, both functionally and in the context of specificity of neural connexions, to warrant brief description.

METHODS

Rhesus monkeys weighing between 1.5 and 2.0 kg were anaesthetized with sodium pentobarbitone and repeated doses of the drug were given, as necessary, to maintain adequate anaesthetic levels. Flaxedil (5 mg/kg.hr) was given to abolish eye movements. Although the positions of the fovea and the optic disk were periodically checked during the course of the experiments, no effort was made to monitor continuously the movement of the eyes as has been done by Hubel & Wiesel (1973) and by Pettigrew (1973). Such information, vital in studies undertaken to demonstrate binocular cortical cells whose receptive fields are in slightly disparate, but fixed, positions in the two eyes, is relatively unimportant when changing disparities are involved, as in this paper. It is therefore unlikely that such information would have modified any of the conclusions reported in this paper. The surgical, recording, stimulation and histological methods have been described in detail elsewhere (Zeki, 1974).

RESULTS

A. Cells having double, and opposed, inputs from one or both eyes

Fig. 1 shows the response of such a cell. This cell was binocularly driven and there was no suggestion of eye dominance in this particular case. The cell gave a powerful response when two edges were moved towards each other within the receptive field (Fig. 1*A*). For such cells, the orientation of the edges was particularly critical and changing the preferred orientation by 15° or more led to a sharp fall in the response of the cell. At 45° to the preferred orientation there was usually no response at all (Fig. 1*E*). Moving just one, appropriately orientated edge in the appropriate direction within the receptive field elicited minimal activity (Fig. 1*C*) and the cell responded weakly, if at all, to an appropriately orientated slit moving

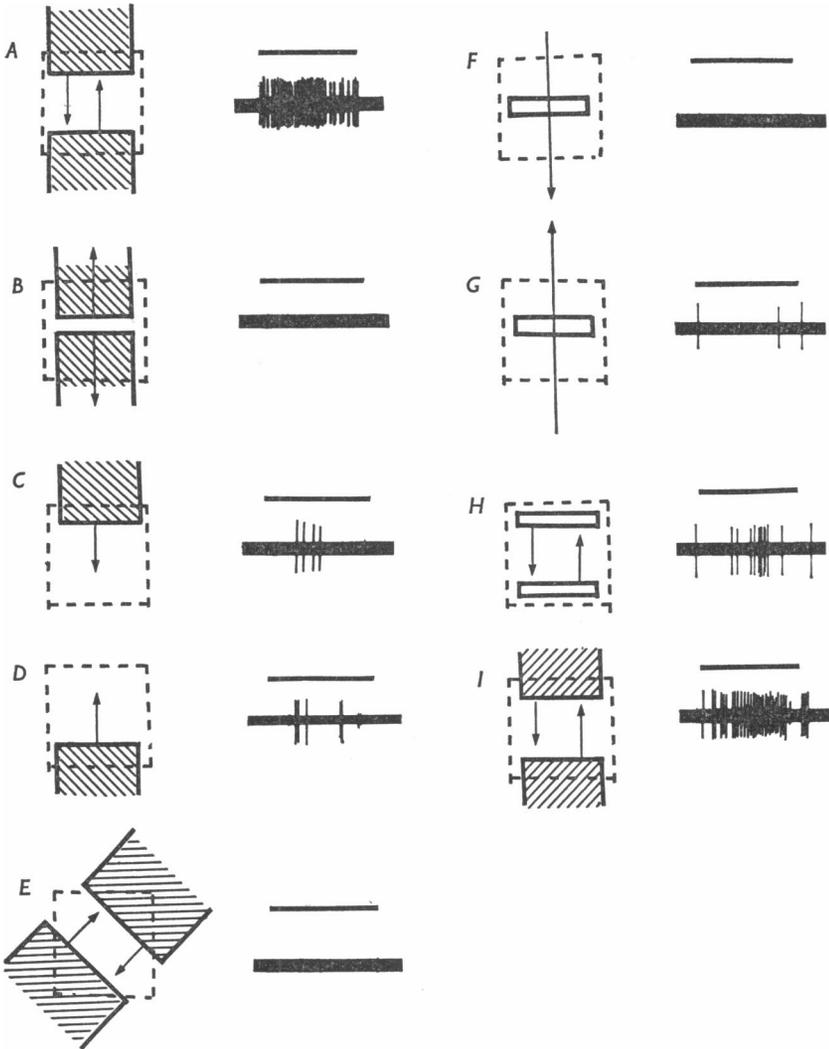


Fig. 1. The response of a binocularly driven cell in the cortex of the posterior bank of the superior temporal sulcus to stimulation of the right (ipsilateral) eye. The cell gave a powerful response when two dark edges of the same orientation were moved towards each other within the receptive field. The edges were generated by opening and shutting the variable diaphragm interposed in the light path. Movement of the two edges away from each other was ineffective (*B*). Movement of one edge only in the appropriate direction elicited minimal activity (*C*, *D*) and movement of slits of the appropriate orientation (*F*, *G*) was ineffective. Movement of two appropriately orientated slits in the appropriate directions within the receptive field (*H*) elicited some activity but this was not as powerful as movement of two edges (*A*, *I*). Background and edges $\log 1.5 \text{ cd/m}^2$, intensity of the stimulus varied from 0.5 to 2.0 log units above background. The size of the receptive field was $5^\circ \times 5^\circ$ and it was located in the lower contralateral quadrant, including the fovea. Duration of each sweep about 4 sec, with the line above each record indicating when the stimulus was moved across the receptive field.

perpendicular to its axis (Fig. 1*F, G*). The cell did not respond when two edges were moved away from each other, even if the edges were of the appropriate orientation (Fig. 1*B*). However, other cells responded only to motion of two edges away from each other, in diametrically opposite directions, although they otherwise had the same properties described above. The receptive field axes of both sets of cells varied in different penetrations and there was no suggestion that any one orientation was preferred over the others. Changing the length of the edges beyond the receptive field boundaries did not change the response vigour of the cell. These cells, therefore, behaved much like the complex cells of Hubel &

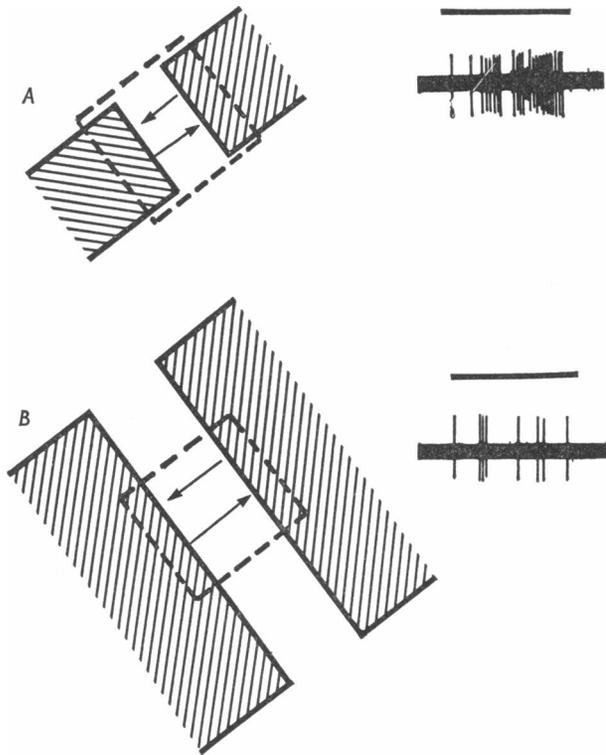


Fig. 2. The response of a binocularly driven, opposed movement hypercomplex cell in the cortex of the posterior bank of the superior temporal sulcus to stimulation of the right (ipsilateral) eye. The cell responded when two edges of the appropriate orientation were moved towards each other within the receptive field. Increasing the length of the edges diminished the response (*B*). The cell was $5^\circ \times 4^\circ$ and was located in the lower contralateral quadrant and crossed the mid line. Background and edges $\log 1.5 \text{ cd/m}^2$, intensity of the light between the edges 1 log unit above background. Each sweep about 4 sec with the bar above each sweep indicating when the stimulus was moved across the receptive field.

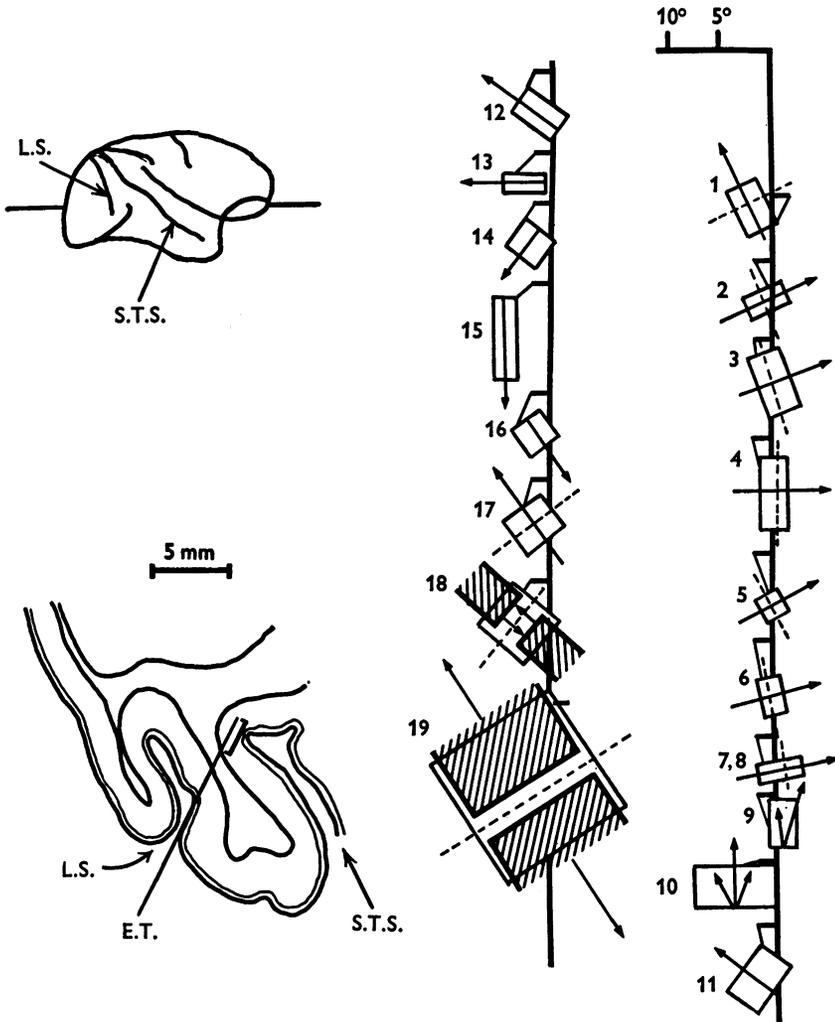


Fig. 3. Reconstruction of an electrode track through the cortex of the posterior bank of the superior temporal sulcus. To the left, a tracing of a horizontal section taken at the level indicated, shows the track. Cells were recovered from the bracketed part of the track. For each cell, the receptive field position is separately indicated with reference to the fovea which is indicated by the intersection of the short horizontal lines with the long common vertical line. The arrows indicate the directional selectivity of the cell. Dashed lines within the receptive field indicate the receptive field axes of the complex cells. Where only an arrow is present, the field belonged to a cell which responded to the appropriate direction irrespective of orientation. Cells 18 and 19 were of the opposed movement complex type, responding to two edges moving in the directions marked. Cells 17, 18 and 19 were all monocularly driven (by the ipsilateral eye only), the remaining cells of the penetration being driven binocularly. L.S. = lunate sulcus; S.T.S. = superior temporal sulcus; E.T. = electrode track. Length of track enclosed in brackets was 1750 μ m.

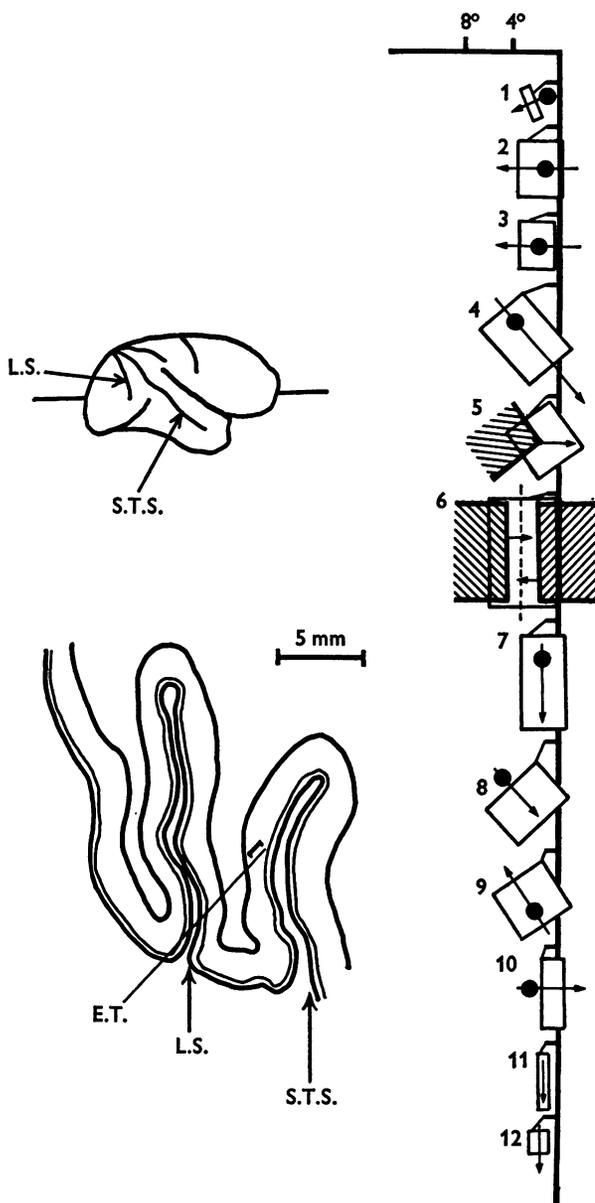


Fig. 4. Reconstruction of an electrode track through the cortex of the posterior bank of the superior temporal sulcus. Conventions as in Fig. 3. Spots indicate that the cell responded best to a spot of light moved in the direction marked. Cell 6 was an opposed movement complex cell. For further details see text. Length of track enclosed in brackets was 3000 μm .

Wiesel (1965) except that they required two appropriately orientated edges moving towards or away from each other in diametrically opposite directions to give an optimal discharge. They may be referred to, *prosaically*, as opposed movement complex cells.

Other cells, while behaving much like the opposed movement complex cells, had even more specific requirements to give an optimal discharge. They may be referred to as the opposed movement hypercomplex cells because of their close resemblance to the hypercomplex cells of Hubel & Wiesel (1965). Such cells not only required that two appropriately orientated edges move towards or away from each other within the receptive field but, in addition, the length of the edges was critical (Fig. 2). Lengthening the edges beyond the excitatory boundaries abolished or markedly diminished the response. What visual information these opposed movement complex and hypercomplex cells may signal is taken up in the Discussion.

Implicit in the response of such cells is a wiring mechanism that is different from that of the common directionally selective cells so often found in this cortical area. It was therefore interesting to learn more about the distribution of such cells in this cortical area, whether, for example, they are grouped together in any particular manner. But penetrations made specifically to study such cells were frustrating because although they yielded the common type of directionally selective cell, cells with the characteristics described above were difficult to come by. Often, as may be seen by reference to Figs. 3 and 4, which illustrate typical penetrations, a single cell or a group of cells with the characteristics described above would be encountered in a penetration rich in directionally selective cells and in many penetrations even this was too much to hope for. A more fortunate penetration is illustrated in Fig. 5. Here several such cells were sequentially encountered. It is of interest to note that the five opposed movement cells, of which four were complex and one hypercomplex, were all grouped together in this penetration. It seems clear, therefore, that the cells may come in groups or clusters but such sequences have been uncommon enough for it to be difficult to say whether the grouping is in the form of columns or not.

Because orientation of the stimulus is so critical for such cells, it was important to note whether in a long, oblique penetration such cells were flanked by directionally selective cells for which the orientation of the stimulus was also critical, since such knowledge may give some idea as to whether local wiring may generate the properties of such cells. The answer seems to be that such opposed movement cells may be flanked by cells having critical requirements for contour or by cells for which contour is not critical. In Fig. 3, the cell immediately preceding the first opposed

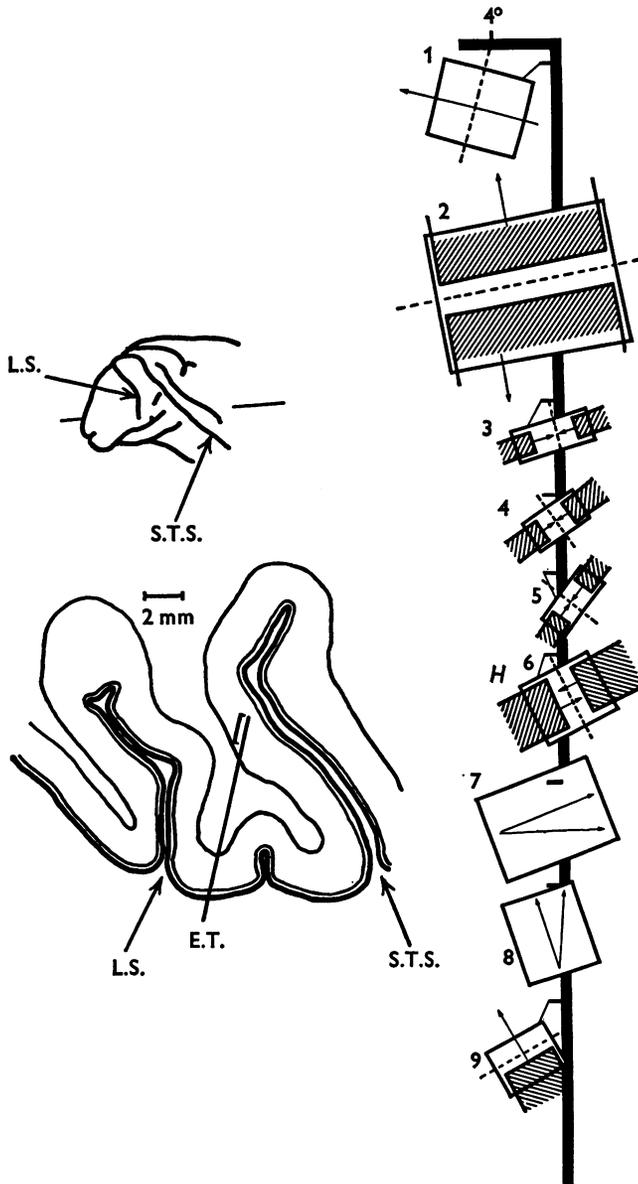


Fig. 5. Reconstruction of a penetration through the cortex of the posterior bank of the superior temporal sulcus. Conventions as in Fig. 3. Cell 2 was an opposed movement complex cell driven by the contralateral eye only; the remaining cells were binocularly driven. Cell 2 responded to two edges moving away from each other within the receptive field. Cells 3, 4 and 5, which were also opposed movement complex cells, responded to two edges moving towards each other. Cell 9 was a complex cell responding to a single edge moved in the direction marked. *H* indicates a hypercomplex field. For further details see text. Length of track enclosed in brackets was 3000 μm .

movement cell (cell 17) was a directionally selective complex cell. In the penetration illustrated in Fig. 4, however, the opposed movement cell was flanked on one side by a directionally selective cell responding best to spots and on the other by a cell, of which this is the only example encountered, responding to a diamond shaped edge moving in the direction indicated. But it is clear, looking at this penetration, that the opposed movement cell was inserted amongst groups of directionally selective cells responding best to spots rather than to appropriately orientated edges or slits. The opposed movement cells of the penetration illustrated in Fig. 5 were flanked on one side by a directionally selective complex cell and on the other by directionally selective cells for which orientation of the stimulus was not critical. It appears, therefore, that in the cortex of the posterior bank of the superior temporal sulcus such cells may come in small groups or clusters and that they may be flanked by cells which have critical requirements for orientation, by cells for which the orientation of the stimulus is not critical or by both types of cell. There is thus no indication from these penetrations that neighbouring cells necessarily had the types of specificity which would contribute towards the specificity of the cells under consideration.

B. Cells having diametrically opposed inputs from the two eyes

Such cells have been found in area 18 of the cat (Pettigrew, 1973) and in the cortex of the posterior bank of the superior temporal sulcus in the monkey (Zeki, 1974). Regan & Beverley (1973) have presented evidence for the existence of such cells in the human cortex. Typically, these cells respond in different, and opposed, ways to stimulation of the two eyes (see Fig. 9, Zeki, 1974). For example, the cell might respond to motion from 3.00 o'clock to 9.00 o'clock for the left eye and from 9.00 o'clock to 3.00 o'clock for the right eye. Such a response, translated into three dimensional space would, of course, mean a response to a slit or bar moving away from the animal (see Figs. 6 and 7). Movement of a slit or bar towards the animal would be signalled by a cell responding to stimulation of the two eyes in just the opposite way to the one described above. Such a type of cell has also been encountered, and in the same penetration (Fig. 6). It should be emphasized that such cells were not always exigent in their requirements for particular contours and for some of these cells a spot appeared to be as effective as a slit in eliciting activity, always providing that the stimulus was moved in opposite directions for the two eyes.

It was, again, important to learn whether there was any grouping of cells with these response properties in the cortex and, if so, what form this grouping takes. In general, the great rarity of this type of cell in this

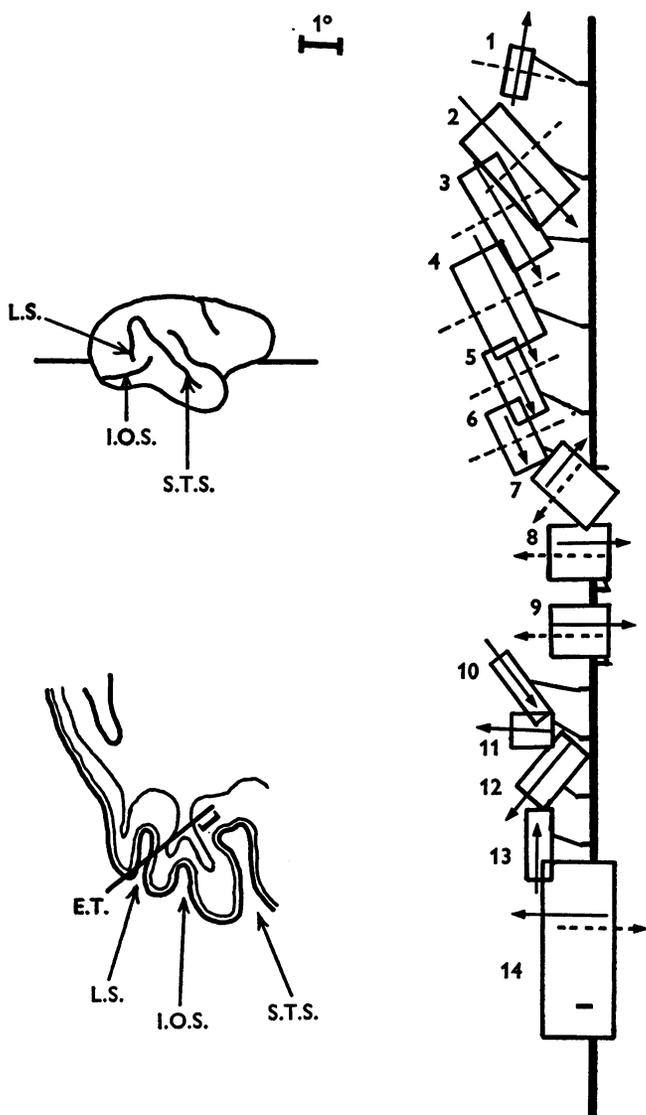


Fig. 6. Reconstruction of an electrode track through the cortex of the posterior bank of the superior temporal sulcus. Conventions as in previous Figures. All the cells in this penetration were binocularly driven but cells 7, 8, 9 and 14 responded in different ways to stimulation of the two eyes. A dashed arrow indicates that the cell responded in that direction when the ipsilateral eye was stimulated, a full arrow means that the cell responded in that direction when the contralateral eye was stimulated. Where only one arrow is shown within the receptive field, the cell was driven identically by the two eyes. I.O.S. = inferior occipital sulcus. Track length enclosed in brackets was 2000 μm .

cortical area (in recordings from hundreds of cells in the cortex of the posterior bank of the superior temporal sulcus, only twelve such cells were encountered) makes this an awkward question to answer at the present time but a hint to their organization may be obtained by reference to Fig. 6. In this penetration four such cells were encountered and, when a unit was isolated, the unresolved background response to stimulation was the same, suggesting that there must be some clustering. It is clear, however, that groups of cells with such properties may, in an oblique penetration, be separated from each other by groups of cells receiving identical inputs from the two eyes. Hence, groups of cells with non-identical and opposite inputs from the two eyes may co-exist, side by side, with groups of cells receiving identical inputs from the two eyes but we have no evidence as to whether the two sets of cells are grouped together into separate columns or not.

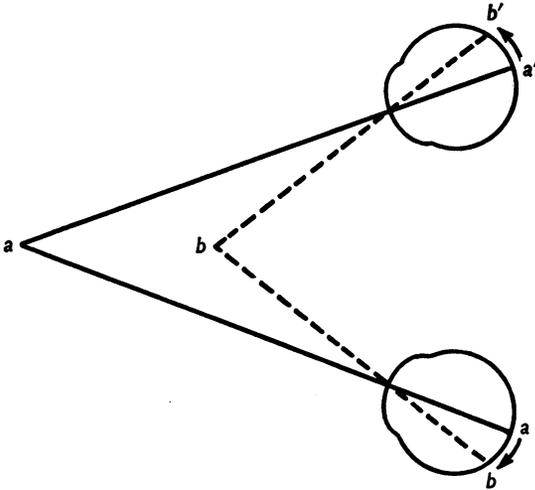


Fig. 7. Diagram to show that when a point a , having its image at a and a' , is displaced to b , having its image at b and b' , the displacement is in opposite directions in the two eyes. For purposes of illustration the distances on the retina in this and subsequent Figures are exaggerated.

DISCUSSION

It would be surprising if, in a cortical area in which motion analysis is emphasized, there were not cells signalling motion towards or away from the animal, information which must be valuable to the monkey. A target moving towards or away from the animal would, necessarily stimulate many retinal points in succession. Consider first the point a in Fig. 7. The image of such a point will fall on a and a' in the two retinas. If the point a is displaced towards b , and hence towards the animal, this will be

tantamount to a displacement to b and b' on the two retinas, assuming the eye positions remain fixed. But as the point moves from a to b , the image of the point will be displaced in opposite directions in the two retinas. Just the opposite would occur when the reverse movement (away from the animal) occurs. To signal the net result, one would simply require a series of retinal

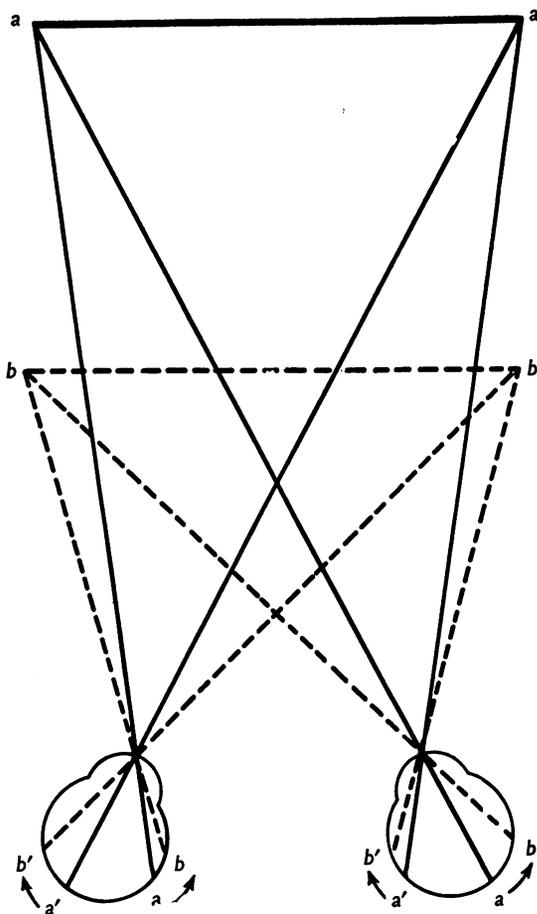


Fig. 8. Diagram to show the displacement of the retinal image when a large bar aa' is moved to bb' . The image will move in opposite directions in each eye. Compare with Fig. 7.

cells in both eyes to be appropriately wired up to a more central cell which, by virtue of its connexions, would discharge when an image is moving in the opposite directions in the two eyes. This is exactly what some of the cells described in this paper do. Of course, the same would apply to a bar with an axis perpendicular to the plane of the paper and to a small hori-

zontal bar moving towards or away from the animal. Hence the relative independence of some cells of this type for contour and orientation. They are, in effect, signalling motion towards or away from the animal, together with the resultant changing disparity. The disparity involved here is quite distinct from the disparity cells of area 18 in the monkey (Hubel & Wiesel, 1970) and the disparity cells seen in cat visual cortex by Barlow, Blake-more & Pettigrew (1967) and by Nikāra, Bishop & Pettigrew (1968). The latter cells respond to fixed disparities whereas the cells described in this paper respond to changing disparities.

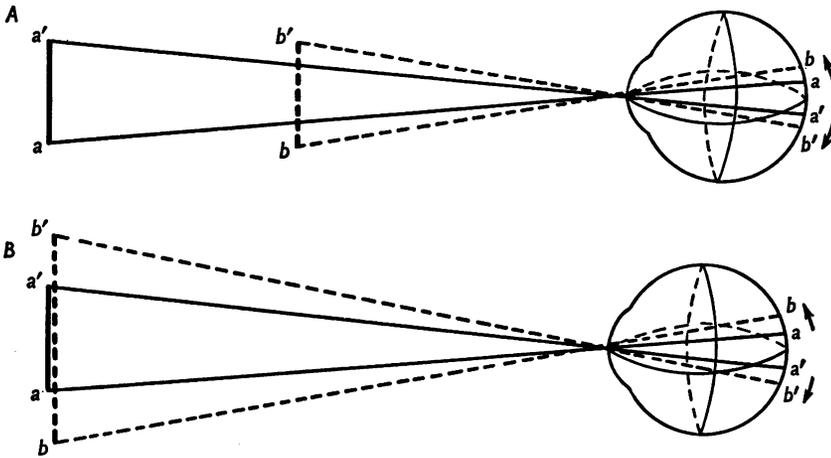


Fig. 9. *A*, when a bar aa' , viewed monocularly, is displaced towards bb' , its image will move in opposite directions across the retina. *B*, the same motion across the retina will take place if, instead of moving towards the eye, aa' becomes enlarged to bb' . For further details, see text.

An examination of Fig. 7 will show that in these cases, one eye alone cannot discriminate movement towards the animal and hence such cells are always binocularly driven. When, however, one considers a larger object, such as is shown in Fig. 8, it becomes immediately apparent that when such an object is displaced centripetally, the displacement of the image on the retina proceeds in a different way and that this can be discriminated by one eye alone (see also Fig. 9). The bar aa' of Fig. 8 has its image on aa' on the right eye and on $a'a$ on the left eye. Displacement of this bar to bb' displaces the retinal image of the bar in two opposite directions in each eye. For a cortical cell to respond to such a displacement, the cell would have to be appropriately connected to retinal cells which will be activated sequentially and in opposed directions for each eye. This is precisely what the opposed movement complex and hypercomplex cells do.

The opposed movement complex and hypercomplex cells may be driven binocularly, or they may be driven by one eye only (see Figs. 3 and 5). Reference to Fig. 9A will show that in monocular viewing, a displacement of a bar aa' to bb' would also lead to a displacement of the retinal image in that eye in two opposite directions. Thus, whether such cells are driven monocularly or binocularly, they would be capable of signalling motion towards or away from the animal.

To signal this type of motion, therefore, both types of cell would be required and it is interesting to note that both types of cell may be found in the cortex of the posterior bank of the superior temporal sulcus. For the opposed movement complex and hypercomplex cells, however, there is a certain ambiguity in the message that they signal, as may be seen by reference to Fig. 9A and B. For a stimulus moved towards the animal would have its image displaced on the retina in just the same way that the image of a stimulus getting larger would be displaced. Other sources of ambiguity may arise from the rotation of objects and from disjunctive eye movements. It is not clear how the cortex differentiates these types of information. Nor is it clear why such cells should be so rare. It is possible that a heavier concentration of such cells may be found in another cortical area.

It is fascinating to note that cells with such specific properties and with response properties implying double and opposed inputs from either the two eyes or from each eye should be so neatly inserted among cells that must have a simpler anatomical wiring, the common directionally selective cells. All this implies a high degree of specificity of connexions, the details of which remain to be worked out. The cortex of the posterior bank of the superior temporal sulcus receives inputs from area 17 as well as from areas 18 and 19 (Cragg, 1969; Zeki, 1971*a* and *b*). Which one of these inputs, or whether all three inputs, play a role in generating the properties of the cells described here remains to be seen.

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