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FUNCTIONAL ORGANIZATION OF A VISUAL AREA IN THE POSTERIOR BANK OF THE SUPERIOR TEMPORAL SULCUS OF THE RHESUS MONKEY

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SUMMARY

1. Anatomical studies have shown the cortex of the posterior bank of the superior temporal sulcus to receive a projection from visual cortical areas, including areas 17, 18 and 19. In this paper the response of single neurones in this area to simple visual stimulation is reported. Ten monkeys were studied.

2. A clear but relatively crude topographic representation of the visual field was found. There was a large variation in the size of the receptive fields of individual cells, even in a single penetration. Some cells, with the central parts of their receptive fields located from between 1 and 5° from the centre of gaze had receptive fields averaging about $10° \times 10°$ or even larger. Other cells with central receptive fields had much smaller field sizes.

3. Two main types of neurones were encountered, with subdivisions within each type. The first type responded to movement irrespective of form. These could be subdivided into neurones which responded to movement in any direction within the receptive field and neurones which responded to movement in one direction only (directionally selective neurones). Another type of cell was responsive to both contour and movement, much like the complex and lower order hypercomplex cells. Almost all such neurones were directionally selective.

4. In oblique penetrations through this cortical region, there tended frequently to be an orderly shift in preferred directions of motion, thus suggesting the possibility of a columnar organization for movement.

5. Combined anatomical (degeneration) and electrophysiological experiments showed that these types of neurones are found in those regions of the posterior bank of the superior temporal sulcus receiving a direct projection from area 17.

INTRODUCTION

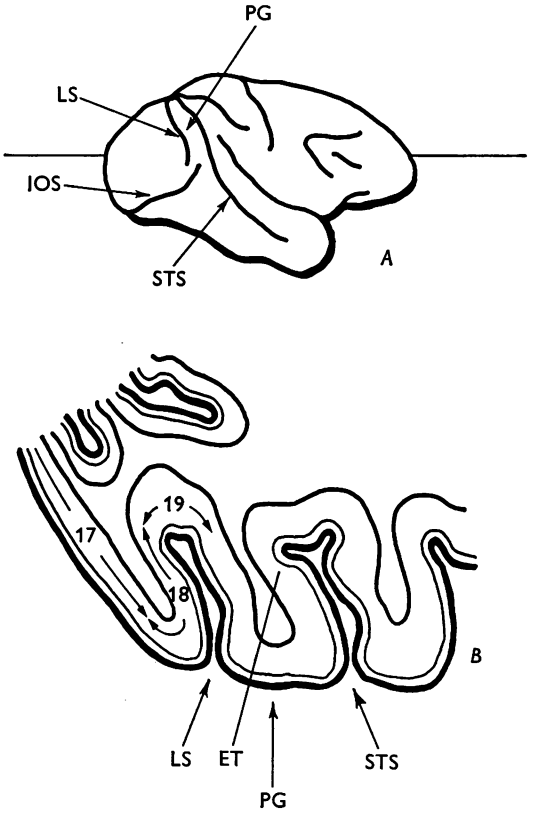
In the monkey, an enormous amount of visual information processing must occur in the cortex. This is implicit in the very large amount of neocortex, extending from the striate area to the inferior temporal areas, that is devoted to vision in this species. Anatomical studies over the past few years have indicated that this cortical area is not a homogeneous field but that it may be subdivided into distinct areas on the basis of an intricate system of anatomical connexions (Cragg, 1969; Zeki, 1969, 1970, 1971*a*). Such a division into a mosaic of anatomically distinct areas is, no doubt, the anatomical basis for a functional division of labour within the visual cortex for handling all the visual information available to the animal, some features of the visual stimulus being emphasized in some areas, other features in other areas, depending upon the organization of the afferent input to each area. Anatomical studies in the visual cortex of the monkey have indicated that a blurring in the detailed topographic representation of the visual field, implied in the term point to point projection, occurs in the projection from the primary visual cortex (area 17) to the cortex of the posterior bank of the superior temporal sulcus. This appeared to be a region receiving a convergent, overlapping input from regions of central visual field representation in area 17 (Zeki, 1971*b*) and it seemed worth while to pursue electrophysiological studies begun earlier (Dubner & Zeki, 1971) and to study the response properties of single neurones in this area to simple visual stimulation as a preliminary attempt in studying the functional counterpart of the anatomical organization in the prestriate cortex of the rhesus monkey.

METHODS

Rhesus monkeys weighing 1·5–2·0 kg were used. The animals were anaesthetized with sodium pentobarbitone and additional doses of the drug were given as required. Flaxedil (5 mg/kg.hr) was given to abolish eye movements. The pupils were dilated by using a solution of atropine and the corneas prevented from drying by placing neutral contact lenses on the cornea. A slit retinoscope was used to determine the power of additional lenses required to bring images on a screen 114 cm away to a focus on the retina. The positions of the optic disk and the fovea were marked on the screen by using a reversible ophthalmoscope and these positions were periodically checked during the course of the experiment. A hole was drilled in the skull over the appropriate region, the dura was reflected and a plastic chamber placed over the defect. The chamber was filled with a solution of 2 % agar-in-saline, thereby providing a closed but transparent system. Recording was through gold-platinum plated tungsten-in-glass microelectrodes (Merrill & Ainsworth, 1972) with an exposed tip of 10–12 μm, driven into the cortex by means of a micromanipulator. The cortex of the posterior bank of the superior temporal sulcus was approached through the prelunate gyrus (see Text-fig. 1). A conventional

recording set-up was used and the signals were fed into an oscilloscope and a loudspeaker. The presence and intensity of the response was monitored by listening to the loudspeaker.

A hand-held projector fitted with an adjustable, rectangular diaphragm was used to project stimuli upon the screen. The stimuli consisted of slits, bars, edges and spots. The light source was a 150 W tungsten filament bulb and the intensity of the stimuli could be decreased by interposing neutral density filters in the light path. Background illumination was normally maintained at 1·5 cd/m^2 and varied as required by means of a calibrated variac. Stimuli were 0·5–2·0 log units above background in intensity. To see whether there was any differential response to wave-length, Wratten gelatin filters or interference filters (Barr and Stroud Ltd) were interposed in the light path.



Text-fig. 1. Tracing of a horizontal section through the brain of the rhesus monkey, at the level indicated in *A*. Only the posterior and lateral part of the section is shown in *B*, to indicate the position of the cortex of the posterior bank of the superior temporal sulcus relative to areas 17, 18 and 19 as these have been determined anatomically for regions of central visual field representation in the rhesus monkey. Most of the penetrations were made through the prelunate gyrus, as indicated. ET = electrode track; LS = lunate sulcus; IOS = inferior occipital sulcus; STS = superior temporal sulcus; PG = prelunate gyrus.

At the termination of the experiments, the monkeys were perfused with normal saline followed by 10% formalin or 4% paraformaldehyde. The brains were sectioned horizontally at 60 μm on a freezing microtome and stained with cresyl violet for Nissl substance to allow a reconstruction of the electrode tracks. In the combined anatomical-physiological experiments, small cortical lesions in area 17 were made 8 and 10 days before the recording experiments, using a fine gauge glass sucker. The dura was then re-approximated, covered with gelfoam and the defect in the skull filled with sterile dental cement to prevent herniation. At the termination of the recording experiments, the animals were sacrificed and the brains were sectioned horizontally at 30 μm (instead of 60 μm) on a freezing microtome. The sections were then stained by the Wiitanen (1970) modification of the Fink & Heimer (1967) staining technique for silver degeneration, which also showed the electrode tracks to advantage. To eliminate the possibility that the degeneration in the sections may have been due to the electrode itself, rather than the lesion, another electrode was put into the posterior bank of the superior temporal sulcus of the opposite hemisphere in the same animal and left there for the duration of the experiment. Both sides of the brain were then stained simultaneously.

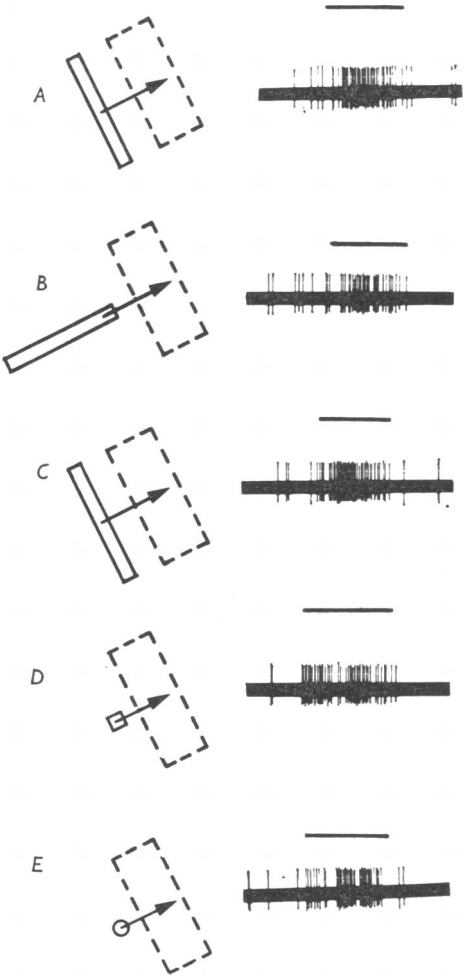
RESULTS

The cells encountered in this region responded to spots of light, bars, edges and slits, usually regardless of wave-length. The majority of the cells were independently driven from the two eyes and there were no marked differences in the organization of the receptive fields for the two eyes. Most cells responded equally well to stimulation of either eye alone, although preferences for one eye or the other were often seen.

For some cells, the shape of the moving stimulus was clearly not very critical nor was the direction of movement of the stimulus. These cells responded well to a stimulus moved in any direction within the receptive field and a small spot of light appeared to be as effective in eliciting a vigorous response as a light or dark bar covering the receptive field. A particularly good response was obtained to jerky movements within the receptive fields. These cells, responding to movement in all directions within their receptive fields, were in a minority and were usually encountered upon first penetrating the cortex from white matter (see Text-fig. 1), although they were occasionally encountered in more superficial layers. In their response to movement in any direction within the receptive field and in their wide tolerance of stimulus shape and size, these cells were reminiscent of the 'pandirectional' cells described by Schiller & Koerner (1971) and by Goldberg & Wurtz (1972) in the monkey superior colliculus.

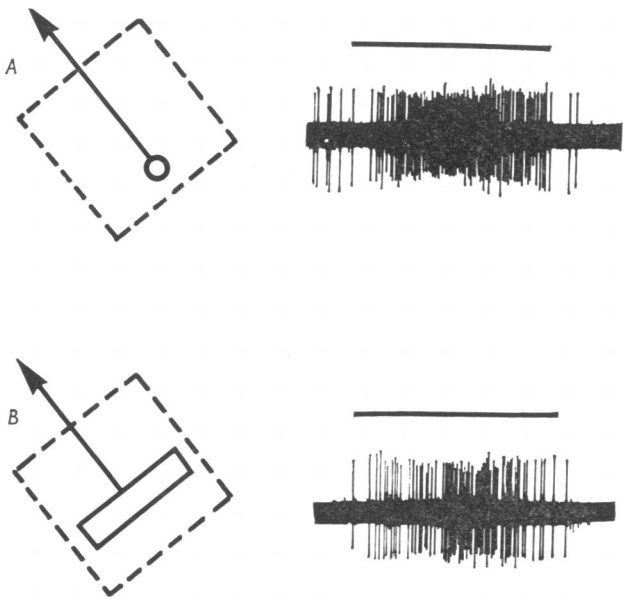
A much more common group of cells had more specific requirements for direction of motion, preferring movement in one direction and not responding at all in the opposite, null, direction. Broadly speaking, such cells could be divided into two groups, one for which the shape of the stimulus or its contrast were irrelevant provided the stimulus was moved

in the appropriate direction, and thus truly directionally selective in the sense described by Barlow, Hill & Levick (1964) and others for which not only the direction of motion but also the shape and orientation of the stimulus were relevant, that is cells comparable to the complex and lower order hypercomplex cells of Hubel & Wiesel (1968).



Text-fig. 2. The response of a cell in the cortex of the posterior bank of the superior temporal sulcus to visual stimulation of the right (ipsilateral) eye. The cell responded to movement in the direction marked by the arrow but not to movement in the opposite direction. The size of the receptive field was $4° \times 11°$ and was located in the lower contralateral quadrant, including the fovea. Background log 1·5 cd/m^2; stimulus 1 log unit above background. Duration of each record approximately 4 sec with the line above each record indicating when the stimulus was moved across the receptive field.

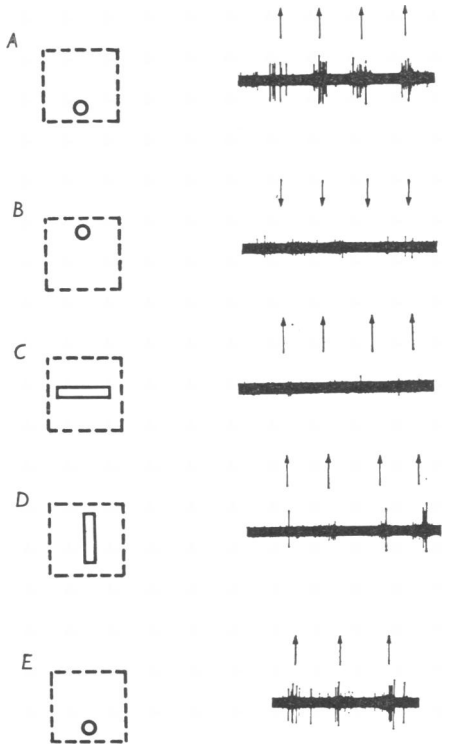
Text-fig. 2 shows a cell which responded to movement from 8.00 o'clock to 2.00 o'clock but showed no response to movement in the opposite direction. Typical of many directionally selective neurones encountered in this region, the cell responded maximally to one direction of motion but tolerated movement at 30° from the preferred axis, the response of the cell decreasing as the deviation from the preferred axis was increased. Movement at 90° to the preferred axis was usually without effect. The cell responded to movement independently of contour, the response being equally vigorous to a small spot of light or a bar covering the



Text-fig. 3. The response of a cell in the cortex of the posterior bank of the superior temporal sulcus to a spot of light (*A*) and to a bar of light (*B*), both moved in the same direction within the receptive field. Stimulation of the right (ipsilateral) eye. The size of the receptive field was 6° × 6° and was located in the lower contralateral quadrant. Background log 1·5 cd/m²; stimulus 1 log unit above background. Duration of each record approximately 3 sec. The line above each record indicates when the stimulus was moved across the receptive field.

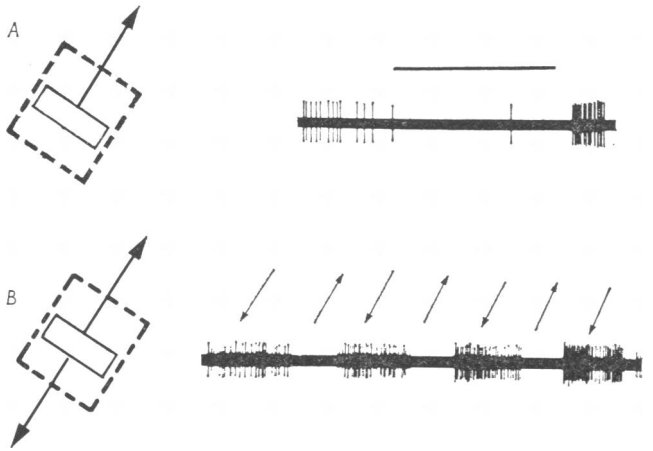
entire receptive field and moving parallel or perpendicular to its axis. Shining the stimulus anywhere within the receptive field and moving it in the appropriate direction elicited a vigorous response. The cell also responded equally well to a black bar moved in the same direction. Thus, for such a cell the actual shape of the moving stimulus was irrelevant provided it moved in the appropriate direction and summation of the response from the simultaneous stimulation of many parts of the receptive

field could not be demonstrated (see Text-fig. 2). Indeed, frequently a small spot of light moved in the appropriate direction was more effective than a bar of light covering the entire receptive field (see Text-fig. 3), almost as though the receptive field had a detailed checkerboard substructure of inhibitory and excitatory areas. An extreme example of this type of cell is shown in Text-fig. 4. The cell responded maximally to a small spot of light moved towards 12.00 o'clock anywhere within the receptive field. Movement towards 6.00 o'clock was without effect. A bar



Text-fig. 4. The response of a cell in the cortex of the posterior bank of the superior temporal sulcus to spots of light (*A*, *B*, *E*) and to bars of light (*C*, *D*). The cell responded to movement of a spot of light towards 12.00 o'clock anywhere within the receptive field (*A*). There was no response to movement towards 6.00 o'clock (*B*). A bar of light covering the receptive field and moving perpendicular to its axis in the preferred direction (*C*) gave no response and a bar of light moving parallel to its axis in the same direction, though yielding a response (*D*), was not as effective as a spot of light (*A*, *E*). Stimulation of left (contralateral) eye. Receptive field was $3° \times 4°$ and was located in the lower contralateral quadrant. Background log 1·5 cd/m^2; stimulus 1 log unit above background. Duration of records *A*–*D* approximately 4 sec, record *E* approximately 3 sec.

moved perpendicular to its axis towards 12.00 o'clock was ineffective, almost as though it was impinging simultaneously on both the excitatory and inhibitory regions within the receptive field. A bar moved parallel to its axis was more effective but not as effective as a spot of light moved in the preferred direction. It was naturally interesting to learn whether the lack of response to movement in the null direction was due to inhibition or simply lack of excitation. For many cells, no inhibition to movement in the null direction could be detected, the cell simply not

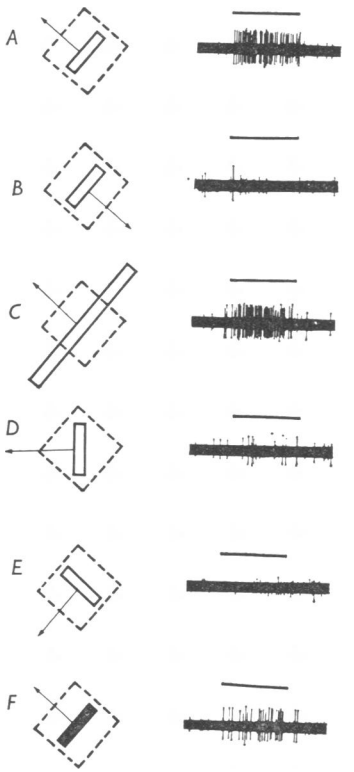


Text-fig. 5. The response of a cell in the cortex of the posterior bank of the superior temporal sulcus to movement in the preferred and null directions. Stimulation of the right (ipsilateral) eye. The cell responded to movement towards 8.00 o'clock but was inhibited by movement in the opposite direction. In *A* the response to movement in the null direction is shown. When the stimulus left the receptive field, there was a marked outburst of firing before the cell regained its spontaneous rate. In *B* the response of the same cell to alternate movement in the preferred and null directions is shown. The receptive field was $4° \times 7°$ and was located in the lower contralateral quadrant, including the fovea. Background log 1·5 cd/m^2; stimulus 1 log unit above background. Duration of upper trace approximately 5 sec, lower trace approximately 15 sec. The line above record *A* indicates when the stimulus was moved across the receptive field.

responding. However, a good many cells were inhibited by movement in the null direction. A typical example is shown in Text-fig. 5. The spontaneous firing of the cell was inhibited by movement in the null direction and, when the stimulus left the receptive field, there was a pronounced burst before the spontaneous activity was resumed. The lower record shows the response of the same cell to alternate movement in the preferred and null directions. The stimulus was moved without leaving the receptive field and following every movement in the preferred

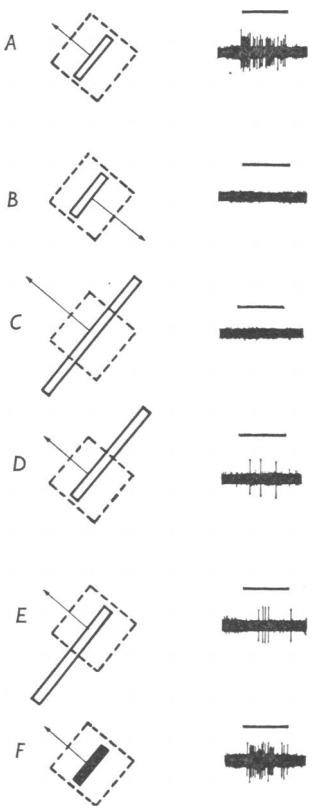
direction, leading to a vigorous discharge, there was movement in the opposite direction, leading to a pronounced inhibition. About one quarter of the cells showed this inhibition in response to movement in the null direction convincingly but this may be an underestimate since a convincing demonstration of inhibition depends upon a good maintained discharge which was not invariably present.

Such cells were common but not all directionally selective cells behaved in this way. For many an optimal response was obtained only when an appropriately orientated stimulus of the appropriate shape was moved



Text-fig. 6. Response of a complex cell in the cortex of the posterior bank of the superior temporal sulcus to a slit of light moved in the preferred (*A*) and null (*B*) directions. Lengthening the slit beyond the boundaries of the receptive field (*C*) did not diminish the response but changing the orientation and direction of motion (*D*, *E*) did. The cell gave a good response to a black bar moved in the preferred direction (*F*). Stimulation of the right (ipsilateral) eye. The receptive field was $3° \times 4°$ and was located in the lower contralateral quadrant. Background log 1·5 cd/m²; stimulus 1 log unit above background; dark bar 0·0 log cd/m². The line above each record indicates when the stimulus was moved across the receptive field. Each sweep approximately 2 sec.

in the appropriate direction, and summation of the response from the simultaneous stimulation of many parts of the receptive field could be demonstrated. These cells, therefore, behaved much more like the complex cells of Hubel & Wiesel (1965, 1968). The orientation of the bar was critical for these cells (see Text-fig. 6) but the degree of tolerance allowed in orientation varied from cell to cell and while for some complex cells changing the orientation by 10° abolished the response or markedly



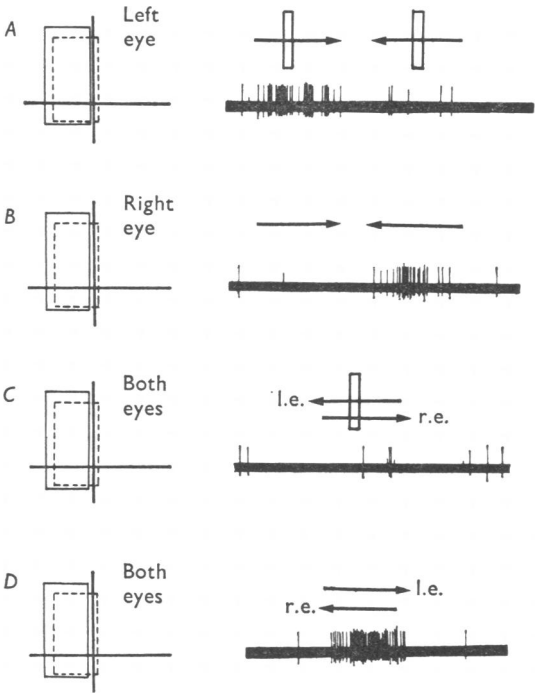
Text-fig. 7. Response of a hypercomplex cell in the cortex of the posterior bank of the superior temporal sulcus to a slit moved in the preferred (*A*) and null (*B*) directions. The length of the slit was critical for eliciting an optimal response and extending the slit beyond the boundaries of the excitatory centre abolished the response (*C*) or greatly diminished it (*D*, *E*). The cell responded equally well to a black bar moved in the preferred direction (*F*). Stimulation of the right (ipsilateral) eye. This cell was recorded in the same penetration as the complex cell illustrated in Text-fig. 6. Excitatory centre of the receptive field was $3° \times 3°$ and was located in the lower contralateral quadrant. Background 1·5 cd/m²; stimulus 1 log unit above background; dark bar 0·0 log cd/m². Each sweep approximately 2 sec.

diminished it, for other complex cells the orientation was less critical and changes in the preferred axis of up to 25° still yielded a powerful response. Yet other cells were still more exigent in their requirements for contour. For these cells not only the shape and orientation of the stimulus were critical in eliciting an optimal response but also the length of the stimulus and extending the stimulus beyond the receptive field boundaries abolished or greatly diminished the response (see Text-fig. 7). In their requirement for a slit or bar of the appropriate length, these cells behaved much like the lower order hypercomplex cells, in area 17 (Hubel & Wiesel, 1968) but were overwhelmingly directionally selective. The number of cells with precise requirements, not only for the direction of motion, but also the shape of the stimulus (that is to say complex and lower order hypercomplex cells) increased in penetrations in which successive cells had their receptive fields within the central 5° of the visual field compared to penetrations in which successive cells had their receptive fields including the central 5° and extending beyond.

Another type of cell, rather more rarely encountered, responded to movement in one direction for one eye and in the opposite direction for the other eye and was analogous to similar cells found in area 18 of the cat by Pettigrew (1973). For such cells, the maximal response was obtained when the stimulus was moved in the opposite direction for the two eyes (see Text-fig. 8). Simultaneous movement in the null direction for the two eyes did not yield any response. Presumably this type of cell, responding to movement in one direction for one eye and in the opposite direction for the other eye, signals movement towards or away from the animal. These cells were not always exigent in their requirements for shape and a small bar of light covering a small portion of the receptive field was frequently as effective in eliciting a response as a bar covering the entire receptive field. A variety of cells may, therefore, be encountered in this region, all of which are responsive to movement and the overwhelming majority of which are directionally selective. A more detailed study, using more sophisticated measuring techniques, will no doubt reveal several subgroups within each category described here.

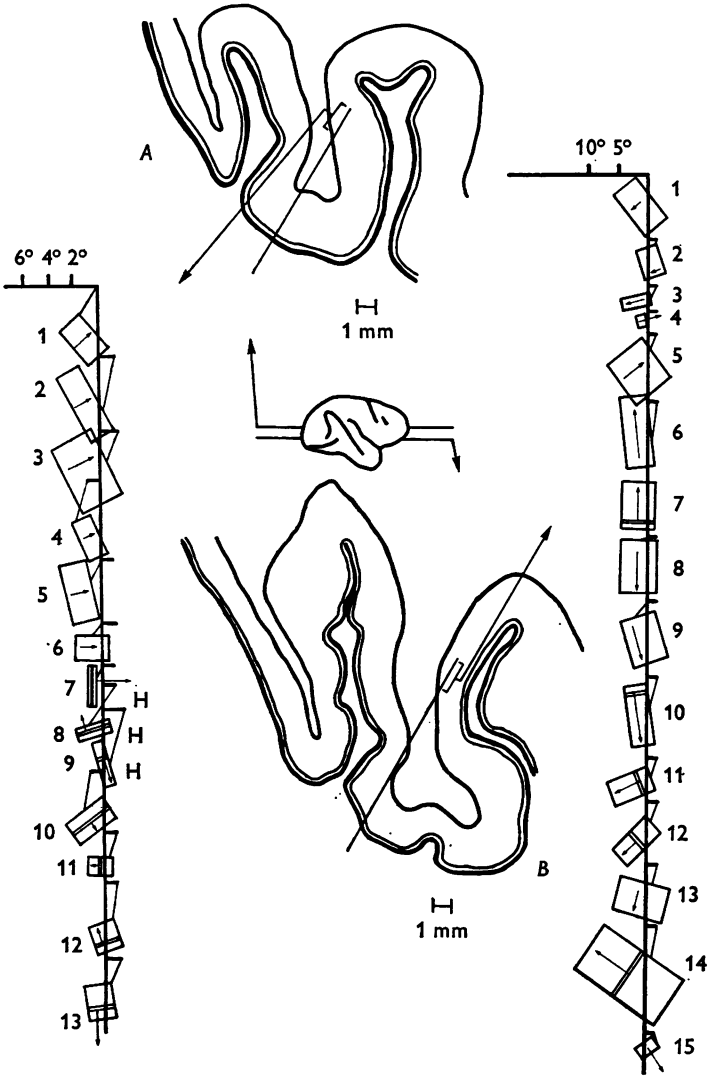
Representative penetrations through the cortex of the posterior bank of the superior temporal sulcus. Text-fig. 9 shows two penetrations through this region, each one in a different brain. In *A*, thirteen cells in a single penetration were recorded. Cells 1 to 6 in this penetration were typical of cells in this cortical region. They were directionally selective in the direction marked by the arrow but the shape of the stimulus was relatively unimportant and summation within the receptive field could not be demonstrated. For these cells a large bar of light, the length of the receptive field, was as effective as a small spot of light and frequently

an equally good response was obtained when a black bar was moved in the preferred direction, although some cells responded more grudgingly to a black bar. Indeed, for cells 5 and 6 movement of a tiny spot of light across the receptive field elicited a more vigorous response than movement of a bar or slit of light the length of the receptive field, a common finding with such cells. At cell 7, not only the receptive field size but the



Text-fig. 8. The response of a cell in the cortex of the posterior bank of the superior temporal sulcus to stimulation of the two eyes. The receptive field for the ipsilateral (right) eye is marked by the interrupted rectangle, that for the contralateral eye by the solid one. In *A*, stimulation of the contralateral eye by a slit of light moved in the directions marked by the arrows. In *B*, the same for the ipsilateral eye. In *C*, the response to simultaneous movement in the null directions for each eye is shown. In *D*, the response to simultaneous movement of a slit of light in the preferred direction for each eye is shown. Duration of each trace about 5 sec. Receptive field was $4\frac{1}{2}° \times 2°$. Background log 1·5 cd/m²; stimulus 1 log unit above background. l.e. = left eye; r.e. = right eye.

receptive field properties change. Cell 7 adapted after a few presentations and was very exigent in its requirements for shape, orientation and position of the stimulus. It responded to a slit of light of the appropriate length moved in the direction marked. Increasing the length of the slit beyond the edges of the receptive field abolished the response altogether

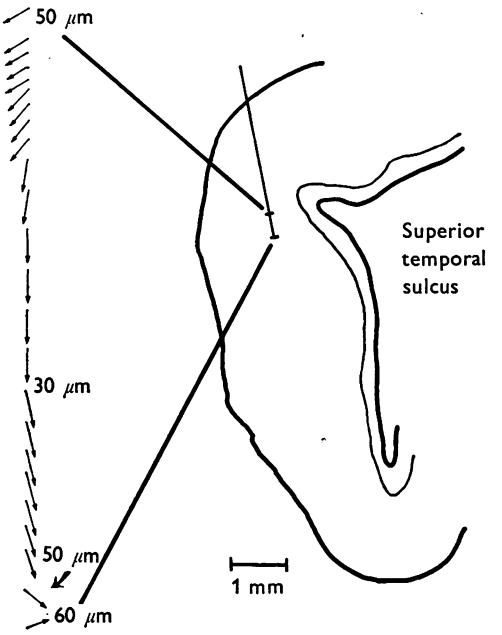


Text-fig. 9. Reconstructions of two electrode tracks through the cortex of the posterior bank of the superior temporal sulcus in two different brains. *A* and *B* are tracings of horizontal sections taken through the brains, at the levels indicated, to show the electrode tracks. For each cell, the receptive 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. Parallel lines within the receptive field indicate that the fields belonged to complex cells, H indicates hypercomplex fields. The arrows indicate the directional selectivity of the cells. Where only an arrow is shown within the receptive field, the field belonged to a cell that responded to movement in the direction marked by the arrow without being exigent in its requirements for contour. Note the progressive change in the preferred direction of motion for cells 1 to 7 in *A* (see also Text-fig. 10). In each case, recording was from the right hemisphere. For further details, see text.

and changing the preferred orientation by 10° diminished or even abolished the response. Thus, in marked contrast to the previous cells, for cell 7 not only the direction of movement but the shape of the stimulus itself became an important stimulus parameter. Cells 8 and 9 behaved much like cell 7 but certain features of the behaviour of cell 9 are worth noting since these have been observed commonly enough in such cells. The cell behaved like a lower order hypercomplex cell in that it responded to a bar of light of the appropriate length moving perpendicular to its axis in the direction marked. Increasing the length of the bar beyond the boundaries of the excitatory receptive field abolished the response. However, the cell gave a powerful response to a bar of light moving parallel to its axis within the receptive field and also to a small spot moved in the preferred direction. In a sense, therefore, this cell was a cross between the hypercomplex cell illustrated in Text-fig. 7 and the cell illustrated in Text-fig. 4. Cells 10 to 13 behaved much more like complex cells. For these cells movement in a particular direction was essential for eliciting an optimal response but the width of the slit was critical and increasing the length of the slit up to the edges of the receptive field increased the vigour of the response. Increasing the length of the slit beyond the borders of the receptive field was without further effect.

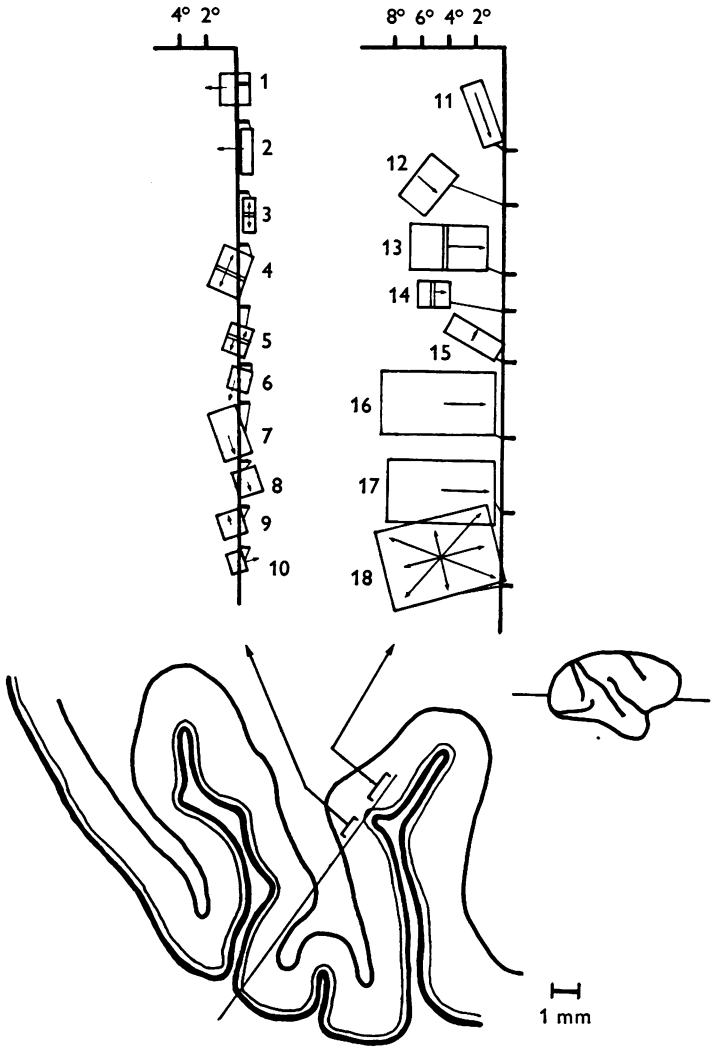
Throughout this and other penetrations reported in this study, there was a tendency for cells of similar response properties to be grouped together. The preferred direction of motion and the orientation for any given cell was the same for the unresolved units audible in the background. Further, as may be seen between cells 1 to 7, there tended to be an orderly shift in the preferred direction of motion, a phenomenon seen repeatedly. A more striking demonstration of this orderly shift in the preferred direction of motion is illustrated in Text-fig. 10. In this penetration, which was almost horizontal to the cortical surface, the preferred directions of motion for successive groups of units were recorded, mostly at intervals of 10 μm. The shift in the preferred direction of motion was gradual and orderly and there was no accompanying shift in receptive field position. There was also evidence of cell grouping according to type. Cells responsive to motion irrespective of form often came in clusters as did complex and hypercomplex cells (see Text-figs. 9 and 11). In penetration *A* of Text-fig. 9, for example, cells 7, 8 and 9 were all of the hypercomplex type. In penetration *B* of Text-fig. 9, cells 10, 11 and 12 were all of the complex type. Whether this clustering is indicative of the segregation of cell types according to layers is not clear. Comparison of perpendicular with parallel penetrations, together with identifying lesions made at the site of particular cell types, would help to resolve the issue.

All the cells in the two penetrations in Text-fig. 9 were studied for their responses to different wave-lengths by interposing Wratten or interference filters in the light path. All the cells in these two penetrations responded to the appropriate stimulus regardless of wave-length and this is the general result for cells studied in other penetrations. Not every cell encountered in this region was studied with light of different wave-lengths but a sufficiently large number of cells was sampled to be sure that the cells of this region are not concerned with wave-length.



Text-fig. 10. Reconstruction of a penetration through the cortex of the posterior bank of the superior temporal sulcus to show the directional selectivity of the successive groups of cells encountered in a single penetration. The electrode track was almost parallel to the cortical surface. Recordings were made from twenty-four groups of cells, most of them at a distance of 10 μm from each other. Where the distance between successive groups of cells was more than 10 μm, this is indicated to the right of the series of arrows. Only the directional selectivity of the successive groups of cells was studied in this penetration. The electrode travelled a total distance of 400 μm and a lesion was passed at the beginning of the track to identify the position histologically. The arrows to the left mark the directional selectivity of the successive groups of cells. To the right is a tracing of a horizontal section through the cortex of the posterior bank of the superior temporal sulcus to show the position of the electrode track. The two horizontal bars on the track mark the region from which recordings were made.

In Text-fig. 11, eighteen cells in a single penetration through the cortex of the posterior bank of the superior temporal sulcus are illustrated. The first ten cells had their receptive fields located in the inferior contra-



Text-fig. 11. Reconstruction of a penetration through the cortex of the posterior bank of the superior temporal sulcus. Conventions as in Text-fig. 9. The receptive fields of the first recorded cells are shown to the left. The electrode then traversed the molecular layer, as seen in Nissl preparations. The receptive fields of the cells recorded after the electrode had traversed the molecular layer are shown to the right. Note the change in receptive field position between the two parts of the penetration. Recording was from the right hemisphere. For further details, see text.

lateral quadrant. After the electrode had traversed the molecular layer, the next eight cells had their receptive fields located in the upper contralateral quandrant, seemingly suggesting a relatively crude topographic organization. It is worth noting in this penetration that cells 3, 4 and 5 responded to movement in two opposite directions. Although the great majority of cells studied in this region were directionally selective, whenever cells responding to two opposite directions were encountered, they occurred in clusters.

Topographic organization. Although the topographic organization was not investigated in detail, Text-figs. 9 and 11 show that there is an orderly representation of the visual field, and therefore presumably an orderly, if relatively crude, topographic organization within this cortical region. This is implied, for example, in Text-fig. 9 where in a single preparation cell after cell had its receptive field located in the same general part of the visual field. It is also evident in Text-fig. 11 where, with the emergence of the electrode from one part of the cortex and its entry into another part after traversing the molecular layer, there was a sudden change in receptive field position from the lower to the upper contralateral quadrant. In a more general sense, this topographical organization is implied in the observation that in any single penetration not only did the cells tend to have their receptive fields located in the superior or inferior contralateral quadrant (with the receptive fields of successive cells in some penetrations crossing the interquadrantic boundary) but that, in addition, they occupied the same general position within the visual field quadrant and any change in receptive field position tended to be orderly rather than abrupt.

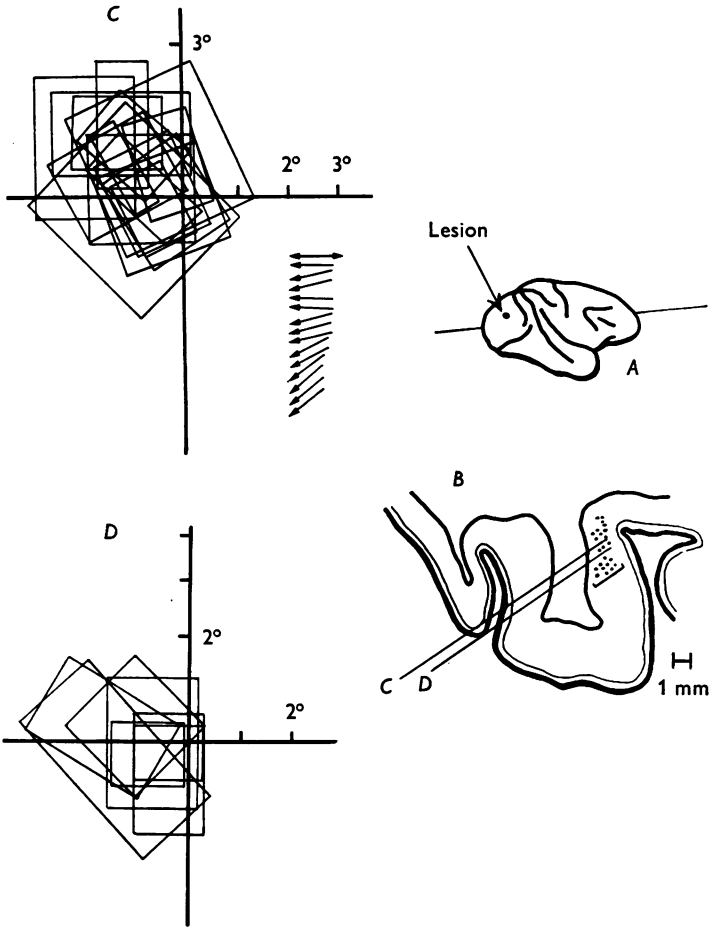
In the observation of central receptive fields large in size compared to central receptive fields in area 17 (Hubel & Wiesel, 1968) the topographic organization within this area appears to be relatively crude compared to the highly detailed topographic map of the visual field in area 17 (Talbot & Marshall, 1941; Daniel & Whitteridge, 1962; Hubel & Wiesel, 1968). Although it was common to find cells with receptive fields ranging from $5° \times 5°$ to $10° \times 20°$ in size (see also Dubner & Zeki, 1971), there was a good deal of variation in receptive field size, even in a single penetration (see Text-fig. 9) with some cells having receptive fields as small as $1° \times 1\frac{1}{2}°$. The cells with small receptive fields had these fields occupying foveal or central positions in the visual field and their presence suggests that a much finer grain visual field representation, together with a coarser one, may exist in this cortical region, at least for the representation of central visual fields. This would be consistent with the known organization of the anatomical input to this area from area 17.

Speed of movement. The speeds to which the cells responded optimally

were not studied in any systematic way and the use of a hand-held projector made it clearly impossible to study this with any degree of accuracy. Nevertheless, by sweeping the appropriate stimuli across the receptive field at different speeds one could get a clear, if not very precise, idea of the order of speeds to which a cell responded preferentially. Our general impression is that there is a range of speeds, from about 5°/sec to about 50°/sec to which the cells responded optimally, some at one extreme preferring very slow speeds while others preferred such fast speeds that it was scarcely possible to plot the receptive field position or size. Most cells were in between and appeared to tolerate a wide range of speeds. There was, however, no evident orderly progression in speed requirements of the individual cells in any particular penetration, the jump from one speed preference to another being more or less random, although in some penetrations sequences of two or three cells preferring fast speeds were seen. Much more accurate quantitative techniques would be needed to see whether there is any grouping of cells according to speeds.

Combined anatomical and physiological experiments. The cortex of the posterior bank of the superior temporal sulcus receives cortical projections not only from area 17 but from cortical areas central to area 17 as well (Zeki, 1969; 1971*a* and unpublished results). Whether the same region of the cortex of the posterior bank of the superior temporal sulcus receives projections from all these areas or whether the projections from the different areas go to contiguous parts of this region is not clear. At any rate, it seemed worth while combining an anatomical experiment with an electrophysiological experiment to determine whether the type of cells encountered in this study is to be found in a cortical area receiving a direct projection from area 17. This would be so if the electrode track and the degeneration following a small lesion restricted to area 17 appeared in the same region of the same section. The presence of an overlapping, convergent projection to this area from area 17 (Zeki, 1971*b*) made such a study possible. A small lesion would disrupt only a small proportion of the afferent input to this area from area 17 but would not, because of the presence of an overlapping input, abolish the response properties of the cells in this area or would do so only to a mild degree. To do this, small lesions were made in area 17 in two monkeys. After survival periods of 8 and 10 days, recordings were made from the cortex of the posterior bank of the superior temporal sulcus of the hemisphere that had suffered a lesion. In both animals cells similar to the ones described in this paper were encountered (see Text-fig. 12). Subsequent histological staining of the sections for silver degeneration (see Methods) showed the electrode tracks and the degeneration in the same region of the same

section (see Text-fig. 12 and Pl. 1), thereby suggesting that the regions of the posterior bank of the superior temporal sulcus receiving a direct projection from area 17 contain the type of cells described in the present study.



Text-fig. 12. Reconstruction of two penetrations through the cortex of the posterior bank of the superior temporal sulcus in an animal with a small lesion restricted to area 17 and made 8 days before the recording experiment. *B* is a tracing of a horizontal section taken through the brain at the level indicated in *A*. The receptive fields of the successive cells in the two penetrations, *C* and *D*, are superposed and separately indicated for each penetration. The black dots in the cortex of the posterior bank of the superior temporal sulcus indicate the area of degeneration in this region following a small lesion in area 17, marked in *A*. Note that the electrode tracks and the degeneration were in the same region of the same section (see also Pl. 1). The arrows in *C* indicate the preferred direction of motion for the successively encountered cells in this penetration.

DISCUSSION

The multiplicity of anatomical areas in the prestriate cortex of the monkey (Cragg, 1969; Zeki, 1969, 1970, 1971*a*) suggests that there is a division of labour within the prestriate cortex as a whole, with the differential wiring to each area dictating what aspect of the visual stimulus is emphasized, what is generalized and what is de-emphasized. Given an area such as the cortex of the posterior bank of the superior temporal sulcus, receiving a direct projection from area 17, one might begin by asking what new functions, not apparent in a study of antecedent cortical areas, are emphasized here. It seems obvious that movement becomes relatively more emphasized here than it is in area 17 or in area 18 (Hubel & Wiesel, 1968, 1970). For in this area not only are directionally selective cells far more common than in area 17 (Hubel & Wiesel, 1968) but, in contrast to area 17, a good many cells respond to movement independently of contour. There are, in addition, cells which respond to movement in any direction within their receptive fields, presumably thereby signalling the presence of movement *per se*, and cells which signal centripetal and centrifugal movement (Text-fig. 9). The possibility of a detailed analysis of the visual fields for movement is also implied in the presence of cells with large receptive fields, together with cells having smaller fields, and in the presence of cells responding to a range of speeds of movement.

As in other cortical areas, the functional emphasis does not occur at random; rather, cells with common preferences appear to be grouped together. In this area, neurones having common preferences for direction of motion were found to be grouped together, with a tendency for an orderly shift in the preferred direction of motion in oblique penetrations, just as the neurones in area 17 are grouped together according to receptive field axes and neurones in area 18 are grouped together according to their depth preferences (Hubel & Wiesel, 1968, 1970). The suggestion seems strong, therefore, that for movement, too, functional columns may exist.

The implications of this work, when taken in conjunction with previous work on area 17 and cortical areas central to area 17 (Hubel & Wiesel, 1968, 1970; Zeki, 1973) are of some interest in the context of the organization of the visual cortex for handling visual information. Campbell (1905) used the term 'visuo-sensory' to describe the striate cortex (area 17) in the monkey. Implicit in this terminology was a theory of cortical organization which conceived of all the stages of sensory analysis as having their terminal locus in area 17, beyond which an analysis of a much higher order is executed, as is implied in the term 'visuo-psychic' which Campbell used to describe the prestriate cortex. The work of

Hubel & Wiesel (1968) on area 17 in the monkey has shown, however, that only a relatively simple region by region analysis of the visual fields for contour is executed in this area, the majority of cells responding to contour even independently of wave-length (Hubel & Wiesel, 1968; Dow & Gouras, 1973). Other sensory aspects of vision appear to be analysed in detail in cortical areas central to area 17 in the rhesus monkey. In area 18, the visual fields are analysed in detail for depth (Hubel & Wiesel, 1970) with no evidence that the cells of this region are particularly interested in colour. The suggestion now seems strong that in another area central to area 17, colour analysis is emphasized with the visual fields being analysed in detail for different wave-lengths (Zeki, 1973). In this paper, evidence has been presented for a further area in which yet another aspect of vision, namely movement, is emphasized. It comes as no surprise, in the light of work over the past five years, that the cells of this region respond to movement independently of wave-length and frequently of contour, for wave-length and contour are analysed in detail elsewhere. The picture that is beginning to emerge, therefore, is one of a mosaic of areas, each with a different functional emphasis. Presumably the visual information analysed in detail in these areas is then assembled at an even more central cortical area.

It is likely that the properties of the cells in cortical areas central to area 17 are conferred upon them by differential projections to each area from area 17, either directly or indirectly, without excluding another input from subcortical centres such as the pulvinar (Cragg, 1969) which may influence the behaviour of cells in a manner as yet undetermined. For the area described in this paper, it would be relatively easy to construct wiring diagrams for the elaboration of the properties of some of the cells, following the example of Hubel & Wiesel (1962, 1968), given the cortical input to the fourth layer of this area (unpublished results) and given the possibility of a functional columnar organization of cells within this cortical area. Directionally selective complex cells and cells responding autonomously of contour could be elaborated by a direct excitatory input from one or more directionally selective complex cells in area 17 and, where inhibition for movement in the null direction obtains, inhibitory inputs may be involved as well. Hypercomplex cells may be elaborated by an excitatory and inhibitory input from the complex cells of area 17 or perhaps such cells could be elaborated from complex cells, not in area 17, but in the same part of the cortex of the posterior bank of the superior temporal sulcus, by assuming an interconnexion of cells in the same functional column, as suggested by Hubel & Wiesel (1965, 1968). There is some evidence to suggest that such interconnexions within columns may occur. Small lesions in this area, restricted to the lower cortical

layers, but including layer 4, which receives the predominant projection from area 17, lead to a pencil of degeneration from the lesion right up to the molecular layer, the degeneration being almost in straight lines (see Plate 2). There is some horizontal spread of degeneration as well but this is not nearly as striking as the vertical spread. In sum, an impressive set of cortical connexions exists to account for the properties of these neurones but the possible role of a direct subcortical input cannot be excluded.

Comparison to the superior colliculus. The efferent projections from this area are no less interesting. In particular, the projection to the intermediate layers of the superior colliculus (unpublished results) where cells have been described which discharge prior to eye movements (Schiller & Stryker, 1972; Wurtz & Goldberg, 1972) raises the possibility that this area, after analysing movement, feeds the information to the superior colliculus and is thereby involved in the execution of eye movements in fixating moving forms and targets. In this context, it is worth noting the relative absence of directionally selective cells in the superior colliculus of the rhesus monkey (Humphrey, 1968; Schiller & Koerner, 1971; Cynader & Berman, 1972; Goldberg & Wurtz, 1972; Schiller & Stryker, 1972) as compared to other species (Sterling & Wickelgren, 1969; Straschill & Hoffman, 1969; Kadoya, Massopust & Wolin, 1971; Michael, 1972) seemingly suggesting that at least one function in other species is corticalized in the rhesus monkey. Thus, the type of neurones that the area described here contains makes it a reasonable candidate for the role of transmitting cortically analysed information on movement to the superior colliculus. But the suggestion must remain a tentative one for the present. Indeed, one is anxious to emphasize that in this study the activity of neurones in only a limited part of the posterior bank of the superior temporal sulcus has been reported. Unpublished anatomical results show that other parts of the cortex of the posterior bank of the superior temporal sulcus receive independent inputs from other cortical areas, outside areas 17 and 18. What role these further projections play remains to be seen.

Comparison to the Clare–Bishop area. The great similarity between this region and the Clare–Bishop area in the cat, as described by Hubel & Wiesel (1969) and Wright (1969) should be emphasized. Both contain complex and lower order hypercomplex cells; both have cells with receptive fields much larger, for comparable parts of the visual field, than receptive fields in area 17; in both, the overwhelming majority of cells are directionally selective; both receive a direct cortical input from area 17 and, finally, both contain cells which are relatively insensitive to form. In sum, a reasonable list of functional and anatomical similarities may be given to suggest that the two areas may be homologous in function

in the two species. Whether there is a similarity between this area and what appears to be, on anatomical grounds, similar areas in other species (Allman & Kaas, 1971; Spatz, Tigges & Tigges, 1972) future studies will, no doubt, reveal.

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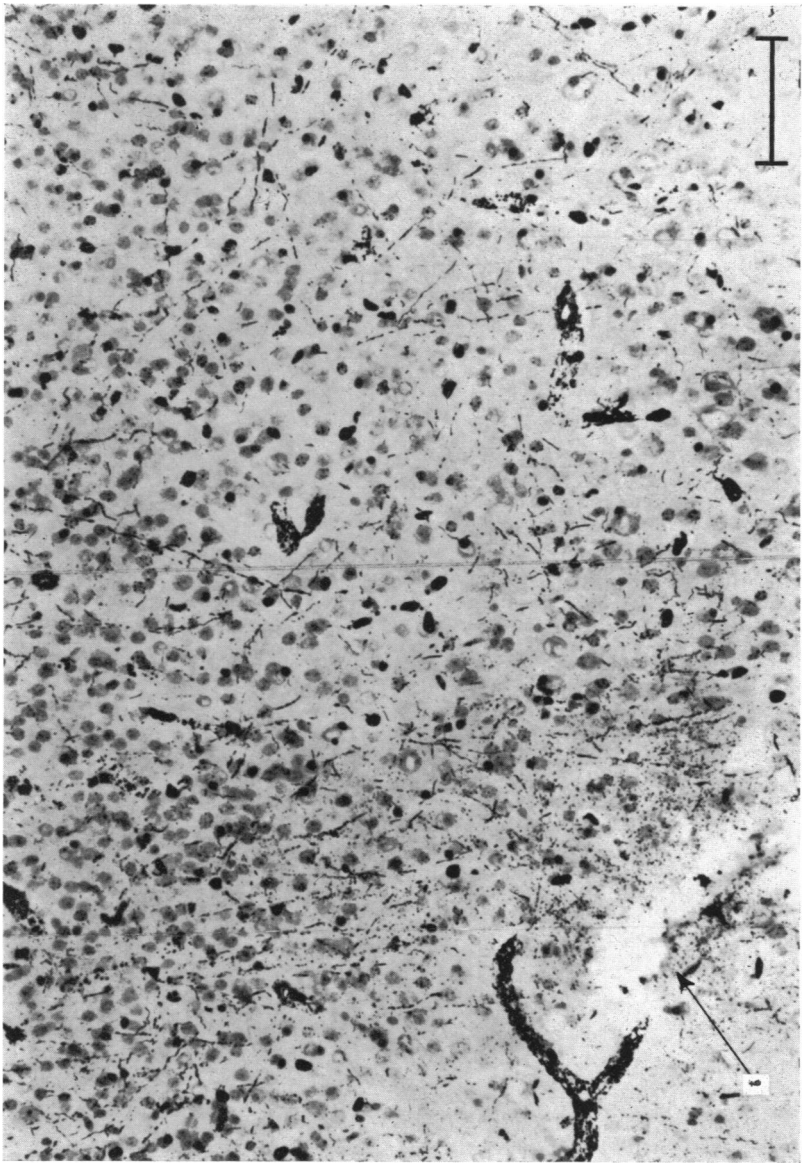
EXPLANATION OF PLATES

PLATE 1

The orthograde degeneration in the cortex of the posterior bank of the superior temporal sulcus and the electrode track made by recording from cells in this region, both seen in the same region of the same section. The degeneration was caused by a small lesion made in the striate cortex 8 days before the recording experiment (see also Text-fig. 12). The recording was made from the hemisphere with the lesion. The experiment yielded cells typical of the cells described in this paper, thus suggesting that such cells are to be found in that part of the cortex of the posterior bank of the superior temporal sulcus receiving a direct cortical projection from area 17. t = electrode track: The scale is 100 μm.



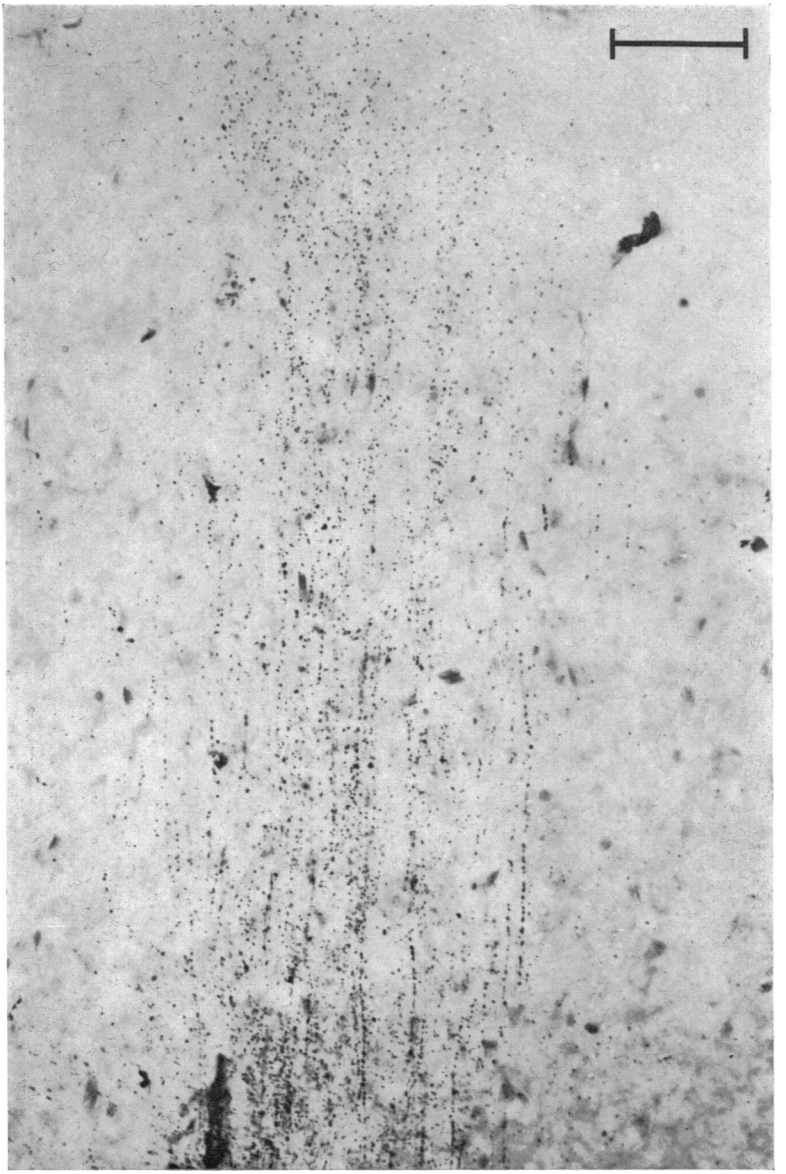


PLATE 2

Columnar degeneration in the cortex of the posterior bank of the superior temporal sulcus. The degeneration was produced by making a small lesion electrolytically in layers 4, 5 and 6, the electrode approaching the cortex from the white matter. Notice the pencil of degeneration streaming towards the molecular layer. Survival time was 8 days. Scale = 100 μm.