The response properties of cells in the middle temporal area (area MT) of owl monkey visual cortex

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Recordings from 178 single cells in the middle temporal area (area MT) of owl monkey showed that most cells there are orientation- and direction-selective. They also revealed that a powerful range of binocular interactions occur in area MT, with 20% of the cells being responsive to binocular stimulation only, 5% to monocular stimulation only and about 50% of all cells showing some degree of interocular interaction.

INTRODUCTION

Over the past few years, studies of the prestriate visual cortex of Macacus rhesus, an Old World monkey, by means of anatomical and physiological techniques, have shown it to be made up of a multiplicity of distinct areas, each specialized to analyse different features of the visual environment (Zeki 1978a, b). It seemed interesting to learn whether the same is true of New World monkeys. The extensive mapping experiments of Allman & Kaas (1975) have shown that in the owl monkey, just as in the rhesus, the prestriate cortex is made up of several areas. Unfortunately, however, these mapping experiments have not been complemented by single cell recordings. Hence the degree of functional specialization, if any, in the prestriate cortex of the owl monkey remains unknown. It was therefore decided to record the activity of single neurons in the visual areas of this animal. In this paper, the results of recordings from one of these areas are reported. The area was one lying dorso-laterally in the occipito-parietal region, at the posterior end of the superior temporal sulcus. It has been called the ‘middle temporal’ area (area MT) by Allman & Kaas (1971). Several workers have affirmed it to be the ‘homologue’ of the motion area of the superior temporal sulcus in the rhesus monkey (Allman & Kaas 1971; Spatz 1977; Ungerleider & Mishkin 1978; Van Essen 1979).

MATERIALS AND METHODS

Four Bolivian owl monkeys (Aotus trivirgatus), two male and two female, were used in the present study. In two of the animals, the splenium of the corpus callosum had been sectioned before the recordings were made, by means of procedures already described (Zeki 1970). For the recording experiments, as for the operation,
the animals were given 0.2 cm$^3$ of ketamine and then anaesthetized with sodium pentobarbitone. Repeated doses of the latter were given to maintain adequate anaesthetic levels.

The surgical, anatomical and electrophysiological procedures were identical to those used in the rhesus monkey (Zeki 1974). Using the map of Allman & Kaas (1971), I drilled a hole in the skull to expose the upper end of the superior temporal sulcus and cemented a plastic chamber filled with agar-in-saline over the defect. This allowed multiple electrode penetrations to be made, by means of a gold–platinum-plated tungsten-in-glass microelectrode with an exposed tip of 7 μm.

The eyes of the animals were dilated with atropine and neutral contact lenses were placed over the corneas to prevent drying. Auxiliary lenses were added to bring images on a screen 114 cm from the animal to a focus on the retina. The positions of the optic disks were plotted on the screen by means of a reversible ophthalmoscope. Allman & Kaas (1971) have estimated the position of the area centralis to be 20° from the optic disk, and I have used this figure. The exact distance is not, in any event, critical in this study.

At the end of the experiments, the animals were given a lethal overdose of sodium pentobarbitone and sacrificed by transcardial perfusion with physiologic saline, followed by a 4 % (by volume) solution of buffered paraformaldehyde. The brains were then sectioned horizontally and stained by cresyl violet for Nissl substance and by the Wütanen (1969) method for fibre degeneration.

Results

Because of the suggestion that the two areas are ‘homologous’, one naturally supposed that the type of stimulus effective in driving cells of the motion area in the rhesus monkey would also be effective in driving cells of area MT of owl monkey. In the former, most cells are binocularly driven and directionally selective, and most respond irrespective of the contour of the stimulus (Zeki 1974, 1978a, b).

It was surprising to find that cells of area MT of owl monkeys were a good deal more exigent in their requirements for optimal stimulation. This made the initial penetrations frustrating, with cell after cell either not responding, or doing so in a vague manner, quite unlike the powerful outburst of cells of the motion area in response to the same stimuli. It soon became apparent that, for a majority of cells, direction of motion was not the only requirement; the orientation of the moving stimulus was just as important. In addition, there were powerful interocular interactions, not hinted at by a study of the cells of the motion area.

(a) Orientation and direction selectivity

Of the 178 cells studied, 76 % were directionally selective, responding vigorously to movement in one direction within their receptive field and either not responding to or, in a few instances, being inhibited by movement in the opposite direction.
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Of these, as many as 71% were orientation-selective as well. For these, even the width of the orientated line was often surprisingly critical, some cells responding exclusively to narrow slits, others to larger ones. As an extreme example, a cell with a receptive field measuring $10^\circ \times 15^\circ$ gave a powerful discharge to a slit $\frac{1}{6}^\circ$ in width but was unresponsive to a slit $1\frac{1}{6}^\circ$ in width. For these orientation-selective cells, a small or large spot of light, or an identical slit orthogonal to the preferred orientation was ineffective. The remaining 29% of the directionally selective cells responded to the appropriate direction of motion, irrespective of contour. Among them were few examples of cells that preferred small spots to slits or bars.

The lowest percentage of direction-selective cells that were also orientation-selective was obtained in a penetration yielding 25 cells. Of these, 44% were orientation-selective. The figure was, however, higher in other penetrations with comparable numbers of cells, being 70% in most, and in some as high as 95%.

I compared these results directly with recordings made from single cells in the motion area of rhesus monkey some three months earlier; 155 cells from two rhesus monkeys formed the basis of the comparison. With penetrations yielding comparable numbers of cells, 36% was the highest percentage of cells in any single penetration that were both orientation- and direction-selective. The lowest percentage was 0%. These results are shown in the histogram of figure 1.

Of the remaining 24% of cells in the owl monkey, 11% were bidirectional and 13% responded to motion of any contour in any direction within the receptive field.

![Histogram](image-url)
S. Zeki

(b) Binocular interactions

It was surprising to find a range of binocular interactions in area MT more extensive than anything seen in rhesus monkey motion area by means of the same techniques. Although the majority of cells were equally well driven by either eye,

![Diagram of ocular preference and interaction histogram](image)

**Figure 2.** Ocular preference histogram, A, and ocular interaction histogram, B, for cells of area MT in owl monkey: c., contralateral eye only; c.d., contralateral dominated; b., binocular; i.d., ipsilateral dominated; i., ipsilateral eye only; b.o., binocular only; b.i., inhibited by binocular stimulation. In histogram B, the numbers in brackets indicate the degree of interocular inhibition where negative and of interocular summation where positive.

**Figure 3.** Reconstruction of an electrode penetration through area MT of an owl monkey with a sectioned corpus callosum. The position of the electrode track (e.t.) and the small lesion made at its end, as well as the callosal degeneration (dots), are all shown on the tracing of a horizontal section, taken at the level indicated on the surface drawing of the brain. The individual receptive fields are shown to the left. Receptive fields for contralateral eye only are plotted (unless cells could be activated by simultaneous binocular stimulation only). Fields are plotted with reference to the optic disk (situated about 20° from the vertical meridian). The presence of a bar within the receptive field indicates that it was orientation-selective; arrows indicate directional preferences. ++, Cells activated only by simultaneous binocular stimulation; ----, cells inhibited by simultaneous binocular stimulation. To the lower right is a cumulative receptive field position diagram. The intersection of the two thick lines marks the position of the optic disk. S.t.s., superior temporal sulcus.
Figure 3. For description see opposite.
no less than 20% of the cells could be activated only by simultaneous binocular stimulation. Another 5% behaved in exactly the opposite way, simultaneous binocular stimulation now yielding no response when monococular stimulation had given a powerful discharge (figure 2, A). Even with cells that were equally well driven by either eye, the effect of simultaneous binocular stimulation was not always predictable from the effects of monococular stimulation, some cells being inhibited by binocular stimulation, others giving a more powerful discharge. Of the cells that were equally well driven through either eye when monococularly tested, 32% showed some degree of binocular interaction. This is illustrated in the binocular interaction histogram (Zeki 1979) of figure 2, B. In preparing this histogram, cells were classified into nine groups, according to their binocular interactions. It shows that 42% of cells in area MT of owl monkey showed some degree of binocular interaction. As a comparison, 97% of the 155 cells whose responses were recorded from the motion area of the rhesus monkey responded equally well to either eye and the vigour of response to monococular stimulation was not lower than that to binocular stimulation. The remaining 3% were dominated by one eye (see also Zeki 1979).

I emphasize that cells responding to simultaneous binocular stimulation only, and ones showing a powerful degree of binocular interaction, were found in owl monkeys with and without callosal section. This is in contrast to the effects of callosal section on the binocularity of cells in the Clare–Bishop area of the Siamese cat, described in a companion paper (Zeki & Fries 1980).

(c) Representative penetrations through area MT

Figures 3 and 4 are reconstructions of two penetrations through area MT, one with a high proportion of orientation-selective cells (figure 3), another with a relatively low one (figure 4). They show common features. Chief among these is the grouping of cells having common orientational or directional preferences, the occasional breaks in an orderly sequence, and the distribution of cells with powerful interocular interactions. In the penetration illustrated in figure 3, the first three cells were bidirectional, orientation-selective and responsive only when both eyes were simultaneously stimulated. All the remaining cells, save cell 25, were directionally selective and all, except 5–6 and 21–25, were orientation-selective as well. On the whole, the orientation-selectivity and the direction-selectivity of successive cells, recorded at intervals of about 50–100 μm, did not change abruptly, as the sequence of cells 7–15 and 16–24 demonstrates. There was, however, an abrupt change in directional selectivity between cell 6 and 7, 100 μm apart, and another abrupt change, in both direction and orientation, between cells 15 and 16, 50 μm apart. Superimposed upon these was a change in the degree of interocular interaction. Cell 14, removed by 50 μm from cell 15, was equally well driven by either eye and simultaneous binocular interaction did not yield a much more powerful response than monococular stimulation. Cell 15 could only be activated by
Figure 4. Reconstruction of a penetration through area MT of an owl monkey. Conventions as in figure 3.
simultaneous binocular stimulation. Cell 16, on the other hand, removed by 50 μm from cell 15, could only be activated by monocular stimulation; simultaneous binocular stimulation inhibited the cell. The inhibition was from the contralateral eye, but there were other instances, in other penetrations, where the eyes were mutually inhibiting.

It is worth noting that the electrode track was in a region of sparse degeneration, produced by sectioning the corpus callosum, and many cells had receptive fields extending to the vertical meridian (see also Zeki (1976) and Zeki & Sandeman (1976)). (In the reconstructions of figures 3 and 4, the receptive fields are plotted relative to the optic disk; the vertical meridian is about 20° to the left.)

In the penetration reconstructed in figure 4, the abrupt breaks in sequence of directional selectivities are also evident, for example, between cells 5 and 6 and again between 6 and 7. This penetration also illustrates how cells may be arranged according to their binocular preferences. In the sequence cell 12–20, the first cell responded equally well to stimulation of either eye alone, but its response to simultaneous binocular stimulation was markedly superior (group B** in the binocular interaction histogram). Cell 13 was a binocularly driven cell, but simultaneous binocular stimulation neither enhanced nor depressed the response. Cell 14, on the other hand, removed by 100 μm from cell 13, was inhibited by simultaneous binocular stimulation (group B–2 in the interocular interaction histogram). Cell 15, removed by 100 μm from 14, was driven only by simultaneous binocular stimulation, as were the three succeeding cells. Such cells also occurred in isolation, as, for example, did cell 4.

From penetrations such as these, it was concluded that there is a tendency for an orderly, sequential change, together with occasional abrupt breaks, in directional-selectivity and orientation-selectivity in penetrations oblique to the cortical surface. The pattern of interocular interactions is more difficult to gauge from these penetrations.

Finally, it was found that the more caudal the penetration in area MT, the more central, within the field of view, were the receptive fields of cells. This finding is a confirmation of the map of Allman & Kaas (1971) for this area. However, the large scatter in receptive field position, especially in the penetration of figure 4, is worth noting.

**Discussion**

An analysis of the properties of single cells in area MT of the owl monkey shows that most cells are not only orientation-selective, but also often highly exigent in their preference for a particular slit width and for direction of motion as well. Moreover, a powerful range of binocular interactions occur there. This obviously raises the question of what the functions of area MT are and to what extent the areas of owl monkey prestriate cortex are functionally specialized. The answer is not easy to give, particularly since we have no detailed functional studies of the other visual areas in this nocturnal animal. In trying to give an answer, it
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may be worth comparing the properties of cells described here with those in the prestriate visual areas of the rhesus monkey. To find orientation-selective cells in rhesus monkey in as high a concentration as found in area MT, one would have to record from areas V1, V2, V3 or V3A (Hubel & Wiesel 1968; Zeki 1978a). To find high concentrations of directionally selective cells in rhesus monkey, one would have to record from the motion area of the superior temporal sulcus. Finally, to find anything approaching the range of binocular interactions observed in area MT, one would have to record from areas V3 or V3A (Hubel & Wiesel 1970; Zeki 1978a, b). Hence, area MT shares some similarities with a number of rhesus monkey prestriate areas.

Recently, several authors have suggested that the motion area of rhesus monkey and area MT of owl monkey are homologous, and have taken to referring to the motion area as area MT (Allman & Kaas 1971; Spatz 1977; Ungerleider & Mishkin 1978; Van Essen 1979). What precisely is meant by ‘homology’ in the nervous system has never been clear, but the arguments for considering these two areas to be similar are not compelling. They are based in part on the location of the two areas close to the superior temporal sulcus, although the term MT stands for middle temporal, and the middle temporal gyrus in rhesus monkey is situated far ventrally in the temporal lobe, well away from the motion area. The arguments are also based, in part, on the presence of reciprocal connections between the striate cortex and the motion area (Zeki 1969, 1971; Weller & Kaas 1978) of rhesus monkey and between the striate cortex and area MT (Spatz 1977). This in itself is hardly persuasive, for such reciprocal connections are found between other areas of visual cortex (Tigges et al. 1973). A similarity, used as an argument in favour of ‘homology’ between the two areas, is that both receive their inputs from the lower layers of striate cortex (Spatz 1975; Lund et al. 1976). However, the Clare–Bishop area of the cat, which also has a high concentration of directionally selective cells, receives its input from the upper layers of striate cortex (Gilbert & Kelly 1976), thus raising the question of whether this is a good criterion for ‘homology’. The studies of function reported here show that there are indeed some similarities, but that the differences are as striking. Hence, I see little justification for calling the motion area of the rhesus monkey MT and suggest numbering it in accordance with the nomenclature established for antecedent visual areas of the rhesus monkey (Zeki 1978a).

The presence of orientation- and direction-selective cells, together with a powerful range of binocular interactions, would argue that area MT may have a variety of functions. What these are should become clear once the functions of other visual areas of the owl monkey, in particular area 17, are studied.

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