

Stimulus Versus Eye Movements: Comparison of Neural Activity in the Striate and Prelunate Visual Cortex (A17 and A19) of Trained Rhesus Monkey*

B. Fischer, R. Boch, and M. Bach

Department of Neurophysiology, University of Freiburg, Hansastr. 9, D-7800 Freiburg, Federal Republic of Germany

Summary. Visual responses were recorded from single cells in the parafoveal striate (A17) and prelunate (A19) cortex of awake rhesus monkeys while they were fixating a stationary or moving spot of light in the presence of a moving or stationary stimulus. Retinotopy and stimulus requirements were found to be less strict in A19 as compared to A17. Striate cells preferred slow stimulus movements and displayed a large amount of binocular interaction. Many prelunate cells responded well to fast stimulus movements, all were binocular but only a few showed binocular interaction. In both areas an overall deficit of visual responses during saccadic eye movements was observed which was mostly due to the cells' inability to respond to stimuli moving at saccadic velocities. Only in A19 were there cells which seemed to receive non-sensory signals reducing visual responses during rapid eye movements. We concluded that the prelunate cortex has access to input which does not use the geniculate-striate pathway. The additional observation of presaccadic activation of some cells supports the idea that activity in the prelunate cortex may be associated with events related to visually guided changes of the direction of gaze and/or attention.

Key words: Cortex – Vision – Eye movements – Monkey

While the striate cortex of the rhesus monkey appears to be a well studied structure both anatomically and physiologically, not much is known about the extrastriate cortex. From degeneration studies, however, we know that there are multiple representations of the vertical meridian, and Zeki (1970)

concluded that there are at least 5 other visual areas. Roughly, V2 (= A18) in the posterior bank of lunate sulcus (LS), V3 on the floor and in the anterior bank, V4 and V4a in the anterior bank of LS and at the prelunate gyrus, the lateral part of the posterior bank of the superior temporal sulcus (STS), and a movement area in the medial part of the posterior bank of STS, (probably the homologue of the medial temporal area (MT) of new world monkeys as discussed by van Essen et al. (1980)) which receives direct projections from the striate cortex. Almost all that we know about the behaviour of single cells in the extra-striate cortex beyond area 18 comes from anaesthetized and paralyzed animals. Zeki (1973, 1977) has reported a preponderance of colour-selective cells in the V4-complex and in the lateral part of the posterior bank of STS and has found many directionally selective cells deep in its posterior bank (Zeki 1974).

A basic problem in visual neurophysiology is the question as to how the visual system handles eye movements. Wurtz (1969) has looked at the responses of striate neurons; for the few cells that responded to fast stimulus movements he found about equal responses when the animal made saccades across the stationary stimulus. Single unit activity associated with goal-directed eye movements has been observed in the frontal eye fields by Wurtz and Mohler (1976), in the parietal cortex (area 7) by Robinson and Goldberg (1978) as well as by Mountcastle et al. (1975) and in the superior colliculus of the monkey by Goldberg and Wurtz (1972).

We recorded from cells in a region of the prelunate gyrus (see Fig. 1) belonging to area 19 of Brodmann (1909), which may be identified with parts of the V4-complex as defined by Zeki.

According to Fig. 90 of Brodmann's book (1909) area 19 lies around 18 with the border between them at the prelunate gyrus. He might have meant to place

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Offprint requests to: Prof. Dr. B. Fischer (address see above)

area 19 near the posterior bank and the floor of the superior temporal sulcus (Zeki 1979), whereas the prelunate gyrus belongs to area 18. Since the terminology of the rhesus monkey visual cortex seems difficult to define at present, we decided to use the terms "area 19" and "prelunate cortex" as synonyms for the visual association cortex as depicted at in Fig. 1.

We looked at the retinotopy of this area, at stimulus requirements of single cells and at their binocularity. Each cell was also tested for its capacity to differentiate between stimulus movements during stationary fixation and equivalent eye movements across stationary stimuli. Identical conditions were used to test cells of the striate cortex in the same animal, such that the two areas of the visual cortex could be directly compared. Preliminary results have been presented earlier by Fischer and Baker (1978).

Methods

Training

Three animals (*Macaca mulatta*, 4–5 kg) were trained to fixate a small (0.1°) red spot of light using the dimming paradigm described by Poggio et al. (1977). Animals had to pull a bar within 0.7 s after the appearance of the fixation spot and to hold it for a randomly varying period of time between 1 and 8 s. Then the spot dimmed and the animal had to release the bar within 0.7 s in order to get a reward of water. They also learned to follow the spot when it moved slowly or to refixate it when it was rapidly displaced, ignoring other visual stimuli. After animals had learned the task a head-holding metal piece was permanently implanted under deep barbiturate anaesthesia and training was continued with the head rigidly fixed after recovery from surgery. Finally, a cylindrical metal chamber was permanently implanted onto which an electrode holding device with a microdrive (Narashige Mo 9) could be mounted daily. Two animals received 4 chambers (2 on A19, 2 on A17 of each) and one only three.

Recordings

Glass coated platinum-iridium electrodes, with impedances between 1 and 4 Megohms (measured at 194 Hz) were inserted through the intact dura. These electrodes allowed continuous recording of multiunit activity with good isolation of single action potentials. Spikes were transformed into unit impulses using a window discriminator and were fed to the z-axis of a storage oscilloscope, providing a continuous raster display. The position of the eye contralateral to the recording site was monitored continuously by analysing the reflected image of the infra-red illuminated eye. X- and Y-components of eye movements were displayed together with the raster display on the same storage oscilloscope. The oculometer detected rapid changes of gaze of 0.1° .

Visual Stimulation

White or black bars of adjustable length, width and orientation (Krüger and Fischer 1976) were projected onto a translucent

hemispheric screen 57 cm from the eyes and could be moved back and forth over several degrees at various velocities perpendicular to their orientation. Stimuli could be presented to each eye separately or to both.

Stimuli, fixation spot and eye position were displayed simultaneously on a single TV-monitor using a half mirror in front of the animal and two TV-cameras. Information on stimulus movement, eye position and spikes was stored, together with behavioural events, on a computer disc.

Procedure

Recording chambers were implanted on the prelunate (A19) as well as on the striate (A17) cortex. We collected data from a total of 409 neurons (A19: 238; A17: 171) in 125 penetrations (A19: 83; A17: 42) made in 11 chambers (A19: 6; A17: 5). At the beginning of each penetration the receptive area (MUF) from which the multiunit activity was driven was mapped on the TV-screen by hand-held stimuli. Upon isolation of a single spike, size, orientation, amplitude and velocity of movement of the stimulus were chosen to give the most consistent responses during stationary fixation. Positions of single cell receptive fields were marked on the screen if they were outside the multiunit field (MUF). Each cell was tested for binocularity and binocular interaction by occluding one or the other eye. Finally, the fixation spot was moved in the same way as the stimulus so that the retinal image movements were equivalent, given that the animal made perfect eye movements. Stimulus and eye movements could alternate during single trials.

Anatomical Reconstruction

When an animal was sacrificed, 5 or more pins were inserted into the brain to indicate the position of each recording chamber. Using the cylindrical coordinates of the penetrations within the chambers and typical landmarks (like sulci), entry points and directions of the electrode tracks could be easily reconstructed on serial sections (20 or 40 μ , cresyl violet) of the celloidin-embedded brain. Taking into account shrinkage factors and depth readings from the microdrive, recording sites for most cells could be marked along the tracks. However, we do not feel sufficiently confident to state the exact cytoarchitectural cortical layer from which a given neuron was recorded, since the accuracy along the depth scale might not be any better than $\pm 150 \mu$. On the other hand, it became clear from the reconstructions that we recorded from all layers, with the possible exception of layer I.

Results

1. Regions of Cortex and Visual Field

Electrode penetrations through the intact dura were guided by the stereotaxic coordinates used during implantation of the recording chambers. Actual entry points in A19 of one animal are shown in Fig. 1 by the dots in the photo of a right hemisphere. One penetration was placed anterior to the superior temporal sulcus in the auditory cortex. The continuous and broken lines indicate the two regions of recording from A19 and A17, respectively, taking

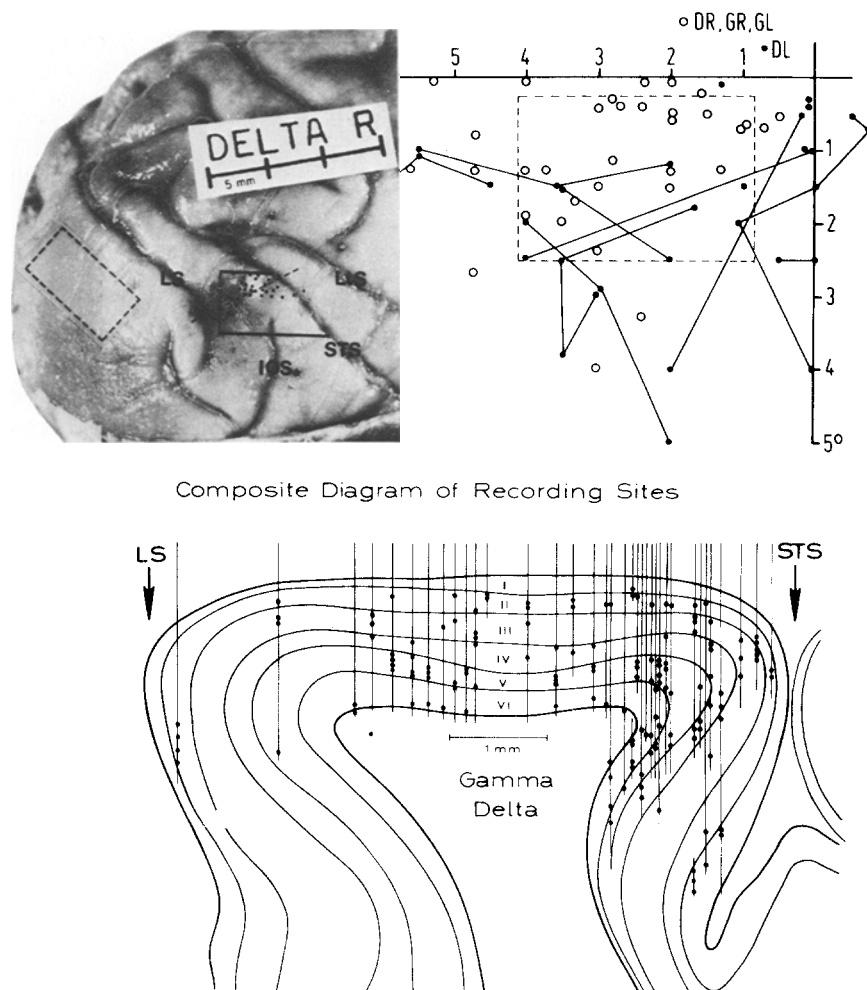


Fig. 1. Upper left: sites of recordings are marked on a lateral view of the right cortical surface by continuous lines for the prelunate and by dashed lines for the striate cortex. Entry points of penetrations in a prelunate chamber are indicated by dots. LS = lunete sulcus; IOS = inferior occipital sulcus; STS = superior temporal sulcus; LtS = lateral sulcus. Upper right: positions of multiunit response fields in the prelunate cortex are marked by circles and receptive fields of individual cells by dots in the lower contralateral quadrant of the visual field. Receptive fields mapped in single penetrations are connected by continuous lines. On the outline of a brain section taken along the broken line across the prelunate gyrus, a number of penetrations are reconstructed and superimposed in relation to their distance from STS

into account all penetrations made in other animals. In Fig. 1 the schematic drawing of a transverse section (along the broken lines in the photo) with superimposed reconstructions of many penetrations shows that we recorded from the prelunate gyrus and the lateral part of the posterior bank of superior temporal sulcus (and not from its medial part). This cortical area represents the parafoveal visual field up to 6° in the lower contralateral quadrant, as can be seen from the upper right diagram of Fig. 1. For each penetration the midpoint of the multiunit response field (MUF) is represented by a circle. In some penetrations receptive fields of single cells were outside the borders of the MUF of that penetration. The positions of these receptive fields are indicated by dots and connected by continuous lines. From the considerable variation of receptive field positions in a single penetration, one has to conclude that there is no strong topographical order (see section 2). The dotted lines on the photo and in the diagram indicate the penetration zone in the striate cortex and the

corresponding MUF positions. Note that both parts of the visual cortex represent about the same part of the visual field, with a greater scatter of receptive fields in A19. In A17 we never found receptive fields outside the MUF mapped once in a given penetration. This observation led us to compare the retinotopic representation in both areas.

2. Retinotopy

As an index of retinotopic precision we used the relation between the cortical distances of pairs of penetrations and the distances of the corresponding pairs of MUFs in the visual field. From the plots of Fig. 2 one concludes that in A17 neighbouring neurons represent neighbouring parts of the visual field within a degree or two, whereas in A19 it is quite common that neighbouring cells represent parts of the visual field with mutual distances of 3–5 degrees corresponding to the dimension of the total

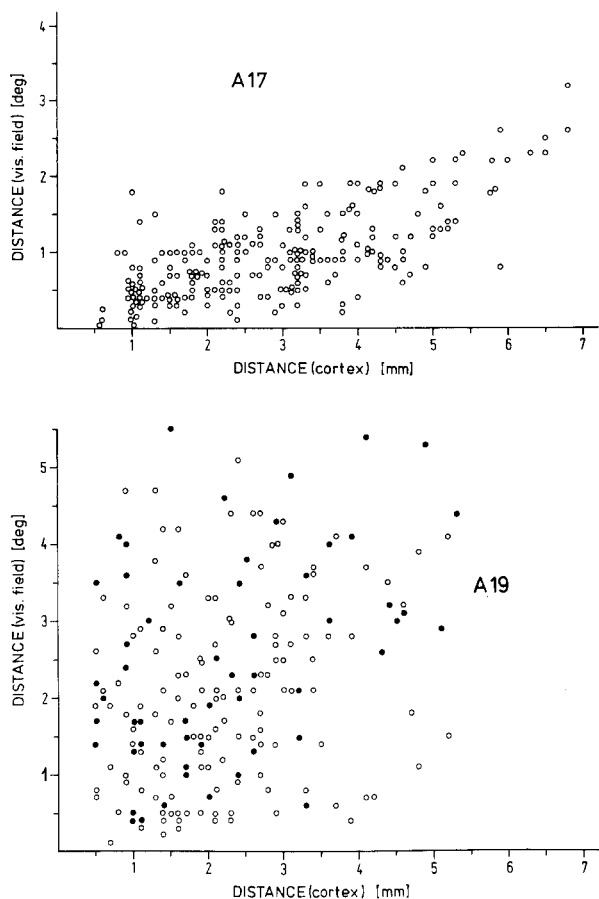


Fig. 2. Comparison of striate (A17) versus prelunate (A19) retinotopic order. The cortical distance of a pair of penetrations is plotted vs. the visual field distance of the corresponding pair of multiunit fields. Black dots in the A19 plot are obtained by considering only those pairs of penetrations whose connecting line runs about parallel to STS

region of visual field representation of this area. Taking into account only those pairs of penetrations (black dots in Fig. 2) that were separated along lines running parallel to the superior temporal sulcus) does not improve the retinotopic order measured by this index. In particular, it still remains the case that response fields of nearby penetrations may be quite distant from each other. Data of Fig. 2 were taken only from penetrations that were perpendicular to the cortical surface.

3. Stimulus Requirements

We first noticed in A19 that almost any stimulus drives multiunit activity, and that its response field, the MUF, was larger by about a factor of 3 in A19 than in A17, where MUFs in our experience are about 0.4 deg wide. Correspondingly, preferred

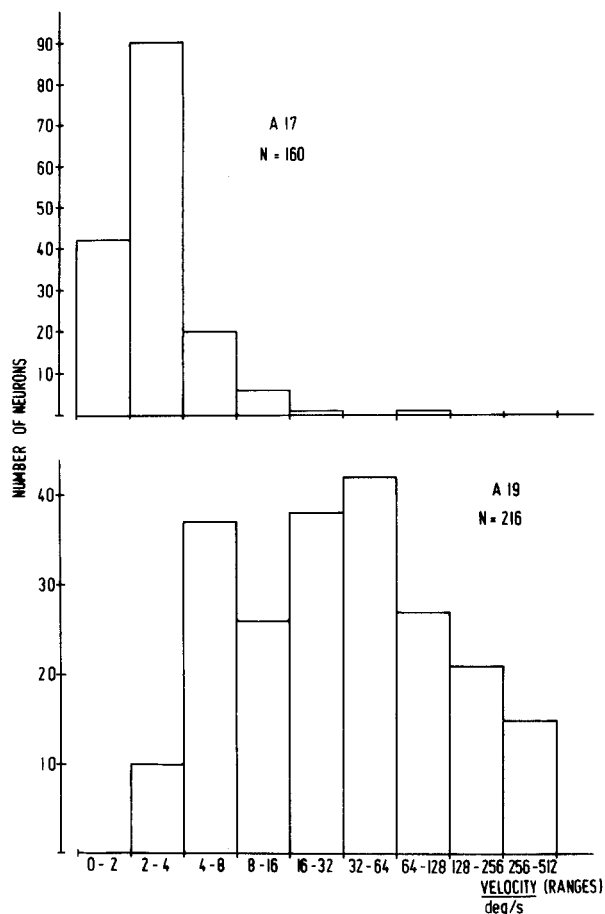


Fig. 3. Numbers of neurons vs. their optimal stimulus velocities indicate the preference of striate neurons for slow movements. In contrast, many prelunate cells responded well at higher velocities where striate cortical cells were no longer responsive

stimulus size and amplitude of movement were also larger by a factor of 3 on the average. As compared with A17, single cells in A19 were relatively unselective for stimulus size, orientation and rate of movement. Directional selectivity, on the other hand, was about the same for the two populations tested. A parameter which was quite critical in A19, however, was the minimal amplitude of movement, which for many cells must be at least 4–6 times as large as the MUF.

The upper histogram of Fig. 3 shows that A17 was most sensitive to stimuli moving at velocities of no more than 8°/s. A19, in contrast, contained many cells that responded most vigorously at higher velocities (up to 500°/s) well beyond the limits of A17 cells.

These optimal velocity profiles of the populations were also reflected in the strength of responses of individual cells in the two areas: confirming earlier observations (Poggio and Fischer 1977), typical stri-

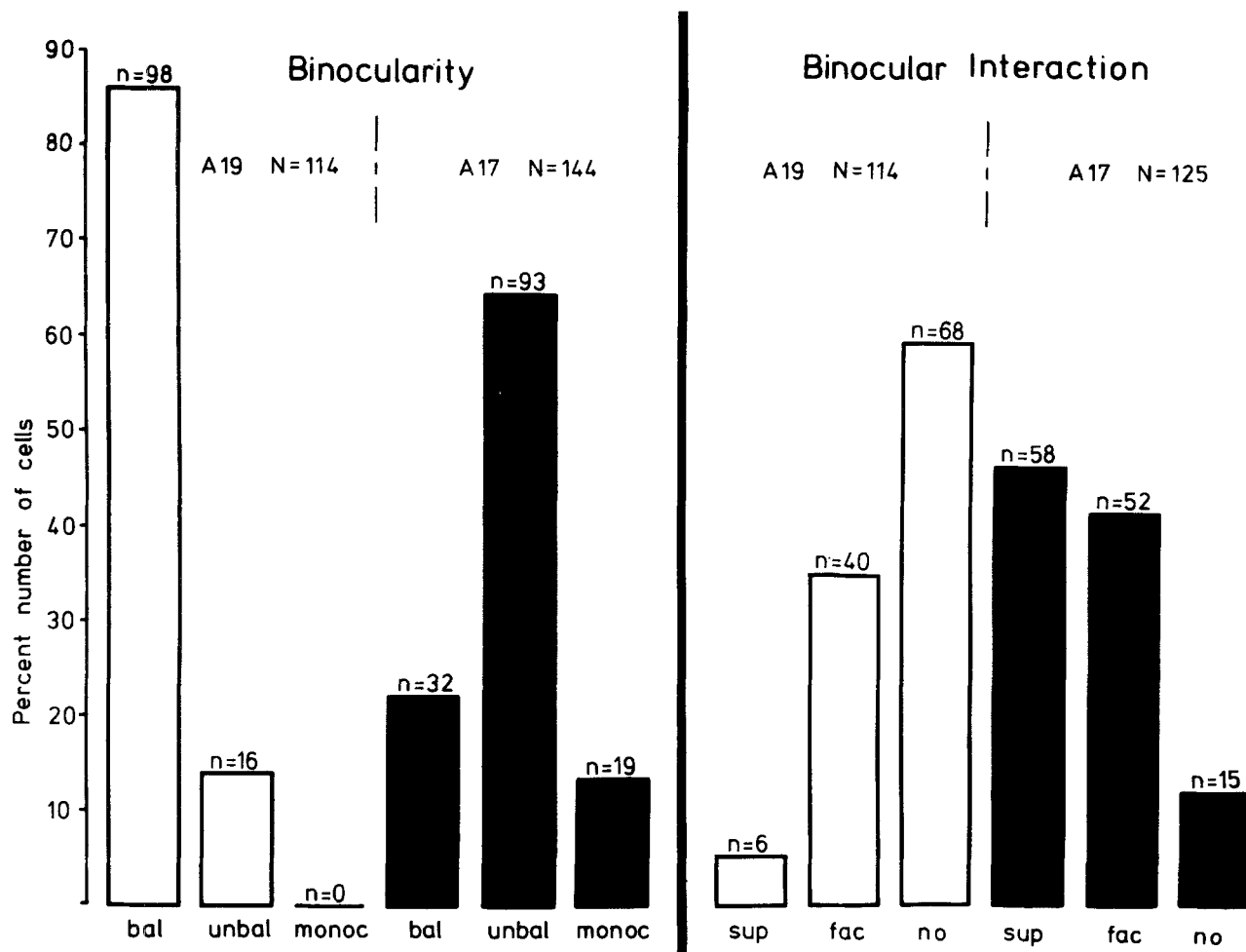


Fig. 4. Comparison of binocularity and binocular interaction in the striate and prelunate cortex. bal = the two monocular responses are about equal; unbal = they are clearly different; monoc = one of the two eyes was unresponsive; sup = the binocular response (stimulus and fixation target at the same distance from the animal) was weaker; fac = the binocular response was stronger; no = the binocular response was equal compared to the stronger of the two monocular responses

ate cells responded to slowly moving stimuli, displayed most consistent and vigorous responses somewhere between 2 and 6°/s and failed to respond at velocities above 16–20°/s. Correspondingly, an A19-cell responded over a much larger range of velocities. The different velocity profiles should be kept in mind when responses to stimulus and eye movements are compared in section 5.

4. Binocularity and Binocular Interaction

With respect to the two eyes, A17 and A19 were quite different. In A19 all cells were driven through each eye separately with a minority displaying differences in monocular responses as judged from the raster displays (see Fig. 4 left). In A17 we found 19 cells with no response from one of the two eyes and the majority of cells displayed ocular imbalance, so

rarely seen in A19. When tested with both eyes open the binocular responses of most A19 cells were the same as their monocular responses, indicating an absence of binocular interaction. Binocular suppression almost never occurred in A19. The opposite was true for A17 cells (black columns at the right of Fig. 4): binocular suppression or facilitation was quite common. Eleven neurons were tested by stimulation at different distances from the eyes corresponding to disparities in a range of ± 1.5 deg. There was no obvious change of their responses. In conclusion: Whatever the function of A19 cells might be, it must be independent of whether the left, the right or both eyes are looking. For the function of A17, on the contrary, interactions between the two eyes and stimulus disparity are quite important, in agreement with earlier observations by Poggio and Fischer (1977).

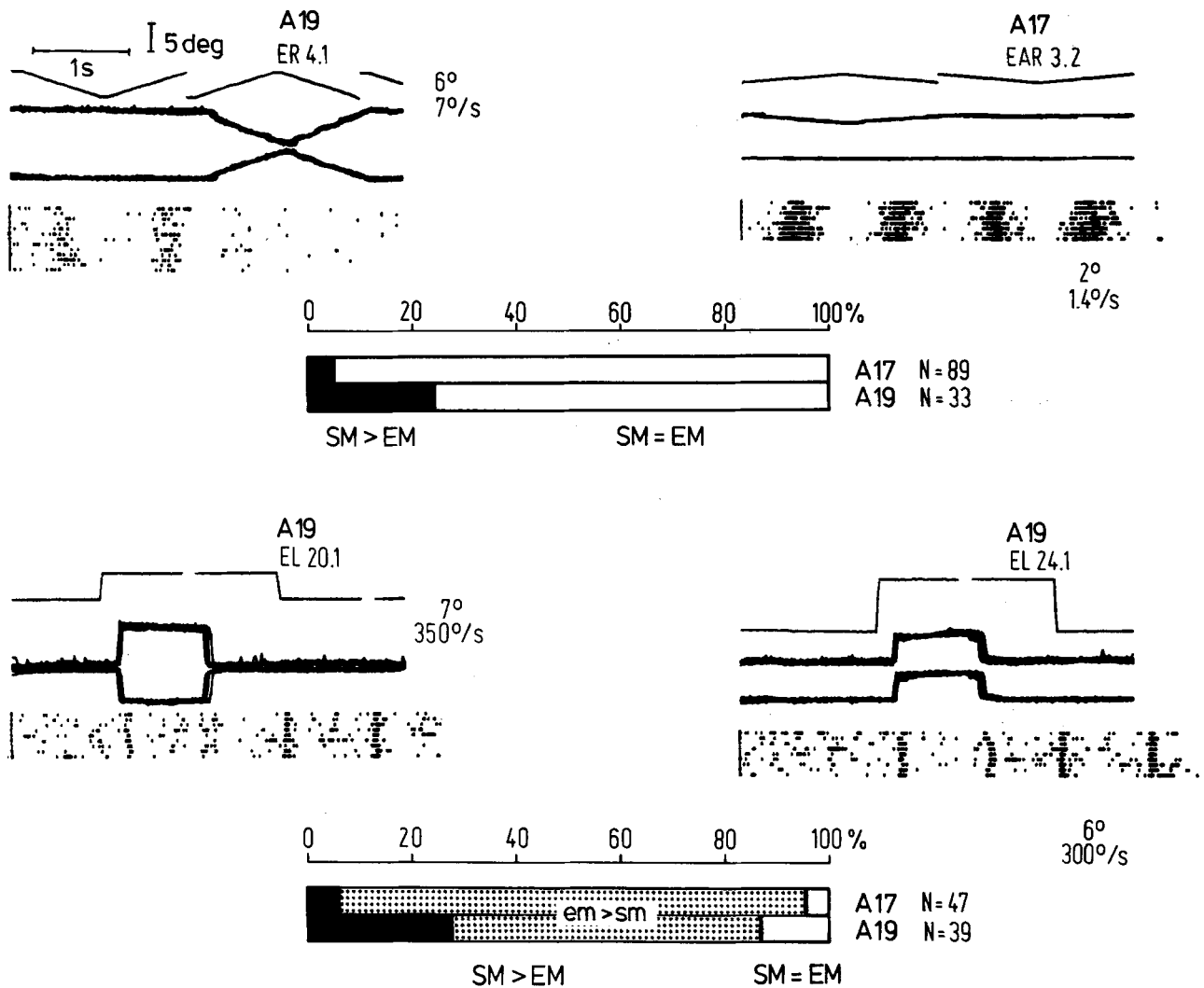


Fig. 5. Comparison of neural activity during stimulus and eye movements. Movements are slow above and fast below. Raster displays of four cells are shown: the two cells at the left responded much less during eye movements, whereas the two cells at the right did not differentiate. SM = responses during stimulus movement; EM = during eye movement. The black and white horizontal bars indicate the percentage of neurons with SM > EM and SM = EM, respectively. For neurons represented by the dotted bars, SM was stronger than EM, but eye movements (em) were faster than stimulus movements (sm) because the animals were unable to track, and executed saccades instead

5. Eye Movements Versus Stimulus Movements

Once a stimulus condition was established that provided the most consistent response from a given cell, we routinely moved the fixation target back and forth once in the first part of a trial, such that the animal had to make corresponding eye movements which displaced the receptive field across the stationary stimulus. In the second part of the trial, the stimulus was moved back and forth in the opposite sense at the same velocity while the animal fixated the stationary spot. Thus, we were able to compare the two responses under conditions of identical retinal stimulation given that the animal made perfect eye

movements. In any event, by watching the TV-monitor we could always see the position of the eye, the stimulus and the fixation spot to make sure that the receptive field really crossed the stimulus during the eye movement. It was also possible to reconstruct the retinal pathway of the stimulus during eye movements using the stored data of x- and y-components of eye position as a function of time.

During evaluation of the data we classified eye movements as "slow" when the animal was able to track the fixation target properly, and as "fast", when the animal made a single saccade or a number of saccades in its attempt to keep the target at the fovea. If a cell would also respond at higher than optimal

rates of movement we often repeated the experiment using fast movements of the same stimulus.

Cells were then classified on the basis of a comparison of their responses to stimulus versus eye movements. The results obtained from 4 representative cells and from pooling the data of the populations are given in Fig. 5. The raster displays at the top were obtained during slow movements and those at the bottom during fast movements. The two cells at the left showed differences in their responses, the two cells on the right responded about equally well during stimulus and eye movements. The black and white horizontal columns indicate the percentages of cells with and without differences in their responses, respectively. The lower pairs of columns is further subdivided according to a comparison of the velocity of eye movements and stimulus movements with the dotted parts corresponding to test situations where the eye moved faster than the target because of the animal's inability to track the target properly. Due to the fact that most striate neurons preferred slow motion and did not respond at "saccadic" stimulus velocities, responses of striate neurons were largely reduced or completely abolished during fast eye movements. But they responded well during slow eye movements. The same seemed to be true for the majority of prelunate neurons, but here we saw a number of cells that clearly failed to respond as consistently during slow or fast eye movements as they did during equivalent stimulus movements (black columns), indicating an inhibitory extraretinal input from an oculomotor structure to these neurons. Note that there was a considerable deficit of neural responses in both areas, when the animal was asked to pursue a fast moving target.

We also recorded from cells that were consistently activated in association with rapid changes of the direction of gaze and which displayed only weak or no visual responses. It turned out that the eye-movement-related responses occurred before the eye had started to move within the saccadic reaction time of about 170 ms. Since eye movements were elicited by displacements of the fixation spot, the latter crossed the retina and reached its final position before the eye had moved and thus served as a visual stimulus. In fact, for 13 of the cells being strongly activated before visually guided saccades, the appropriate stimulus was a small red spot, such that displacements of the (small red) fixation target into the lower contralateral quadrant in the absence of any other stimuli would activate these cells shortly before the eye movement. This observation was made on cells in A19, never in A17. Spontaneous eye movements across a blank screen did not activate these cells. We also noticed that cells of this type

were sometimes encountered one after another in a given penetration.

In conclusion, we have seen at least two sets of neurons: one group, in the striate as well as in the prelunate cortex, was by and large unresponsive during rapid eye movements and another, in the prelunate cortex only, was strongly activated before visually guided eye movements. The exact conditions for activating the latter group of cells remain to be investigated.

6. Further Observations in Prelunate Cortex

In this section we report observations that were made on a few A19 cells only. They were studied by tests used only occasionally or they showed special properties of their activation.

(i) Inhibitory responses were observed in a few cells. Some seemed to have an inhibitory visual input, but all seven cells were clearly inhibited in association with rapid eye movements following displacements of the fixation target. Still other cells were inhibited in association with refixational eye movements, but in addition they had an excitatory visual input. We poorly understand the conditions under which inhibitory responses can be obtained, but it seems clear that events associated with visually guided eye movements can modify the visual properties of many A19 cells quite dramatically.

(ii) Some cells were not movement-sensitive. Instead, they responded much better to the onset of a stationary stimulus or to rapid displacements into rather than across their receptive fields.

(iii) Out of 76 cells tested for colour selectivity using broad-band red, yellow, green or blue coloured filters, 15 responded better to one of them (mostly red) than to black and white, 29 were unselective, and 12 responded differentially to colour stimuli but black or white stimuli were clearly more effective. None of the 20 cells that were unresponsive to achromatic stimuli was driven by coloured stimuli. These observations on colour selectivity appear to be in good agreement with the results of Schein et al. (1980), who used narrow-band equal quantum or photopically matched stimuli.

(iv) Using displacements of a large (150°) global pattern with a 15° × 30° blank area in the middle, we failed to demonstrate the existence of the shift-effect in the striate as well as in the prelunate cortex. What readily activates retinal and geniculate cells in the cat (Fischer et al. 1975; Fischer and Krüger 1974) and in the monkey (Krüger et al. 1975; Krüger 1977), changed neither the on-going activity nor the visually evoked responses of cortical cells.

Discussion

1. Anatomical Implications

The poor retinotopic organisation of the prelunate as compared to the striate cortex and the lack of foveal representation above the tip of the inferior occipital sulcus do not necessarily imply that there is no retinotopic organisation at all. Maybe the fovea is presented more ventrally along the STS. The properties of cells with foveal receptive fields may be different as well. Because of the most evident difference in velocity tuning (many A19 cells responding quite well at high velocities where striate cells are no longer responsive), one may expect that a major input to the prelunate cortex does not use the geniculate-striate pathway, but rather takes the collicular-pulvinar route (Benevento and Rezak 1976), if not still another, more complex afferent pathway. In a recent study, Judge et al. (1980) reported that those cells in the striate cortex responding at high stimulus velocities are mainly found in the infragranular layers which do not project to other cortical areas, but send their fibres down to the lateral geniculate body and the pulvinar. The extraretinal influence that some cells displayed is further evidence that the prelunate cortex is a target of projections that do not arise from the major afferent visual pathways.

2. Functional Implications

From the fact that all cells in the prelunate parafoveal cortex are binocular with balanced input from the two eyes and a considerable lack of binocular interaction, it may be concluded that their functional significance is independent of whether one eye is involved or the other or both, so that they have no relevance in stereopsis and three-dimensional vision. Instead, the visual guidance of conjunctive eye movements or colour vision could be considered, as well as pattern or movement perception. Corresponding to the present results and observations of Schein et al. (1980), however, a major contribution to colour vision is not very likely, because the majority of A19 cells respond well to achromatic stimuli and only a small percentage of them displayed a preference for colour, mostly red. This conclusion could be in contradiction to Zeki's observation (Zeki 1977) of a large preponderance of colour-selective cells in the V4-complex, unless our recordings were made from different parts of the prelunate visual cortex. Since, according to Zeki (1978), it is only the foveal striate cortex which sends fibres directly to V4

and colour vision is well developed predominantly in the fovea, one might not be too surprised to find only few colour cells in the parafoveal prelunate cortex. Nevertheless, the colour-selective cells may have parafoveal receptive fields (Zeki 1973).

In view of the large receptive fields and the poor stimulus selectivity of prelunate cells, a contribution to pattern vision seems unlikely.

The observation of two sets of cells, one being largely unaffected by rapid eye movements across stationary stimuli, the other being activated in association with visually guided eye movements, could be explained by a non-sensory signal arriving at the prelunate cortex before visually triggered changes of the direction of gaze. This signal would inhibit one set of cells and activate the other. The activity of the first set could contribute to vision during stationary fixation and slow pursuit eye movements, whereas the second could contribute to the process of changing the direction of gaze as a consequence of changing the direction of visual attention. Work is in progress in this laboratory to further evaluate the nature of presaccadic activation of prelunate neurons which is quite reminiscent of the enhancement effect of superior colliculus (Goldberg and Wurtz 1972), frontal eye field (Wurtz and Mohler 1976) and posterior parietal cortex neurons (Robinson and Goldberg 1978).

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