Exp Brain Res (1987) 67: 316–322

Experimental Brain Research

Neurons of area 7 activated by both visual stimuli and oculomotor behavior

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Summary. Behavioral and clinical studies have long implicated the posterior parietal cortex of primates in spatial perception and spatially oriented behavior. However, recordings from single neurons in behaving monkeys by different laboratories have resulted in divergent views with some ascribing a largely motor and others a largely sensory role for this region. We have designed paradigms to separate the sensory and motor components of the neural activity and have found that the cells in this area respond to both sensory stimulation and motor behavior. Thus, it is likely that this area is not solely sensory or motor, but rather is involved in higher order aspects of sensory-motor integration.

Key words: Parietal cortex – Visuomotor integration – Eye movements – Fixation – Saccades – Monkey – Area 7 – Efference copy – Corollary discharge – Eye position

Introduction

Several laboratories have made recordings of the activity of single neurons in area 7a of the posterior parietal cortex in behaving monkeys and, by correlating the activity of these cells with sensory and motor events, they have made important advances in understanding its functional role. In the earliest experiments Mountcastle and his colleagues found that many of the cells were activated by certain behaviors of the animal, including saccadic eye movements, fixations, smooth pursuit eye movements, and reaching movements of the arms (Mountcastle et al. 1975). It was stated that these cells did not respond to visual or somatosensory stimuli. On these grounds it was proposed that area 7 was involved in issuing general motor-commands for eye and limb movements.

In later experiments Robinson, Goldberg and colleagues found that many of the cells in area 7 responded to visual or somatic stimuli (Robinson et al. 1978). They argued that the behaviorally related responses reported by Mountcastle and his colleagues could be accounted for either by visual stimulation from the target for movement or from visual/somatosensory stimulation resulting from the movement. It was proposed that area 7a was involved in sensory processes and did not play a role in motor behavior as proposed by Mountcastle and colleagues. In a later report Motter and Mountcastle (1981) noted some cells which appeared to be oculomotor and light sensitive and proposed that a gradient existed between cells with strictly eye movement related responses and cells with solely visual responses.

In the present study we have designed experiments to distinguish between visual and motor components of the responses of the fixation and saccade neurons and have found that the activity of the cells in these two classes is related both to sensory stimuli and to oculomotor behavior. The nature of the eye movement and fixation (eye position) signals suggests that they play a role in establishing spatial constancy rather than in the initiation of oculomotor behavior.

Methods

The activity of single neurons in area 7a and in the lateral wall of the intraparietal sulcus was recorded in two behaving rhesus monkeys while they performed fixation and saccade tasks. The eye

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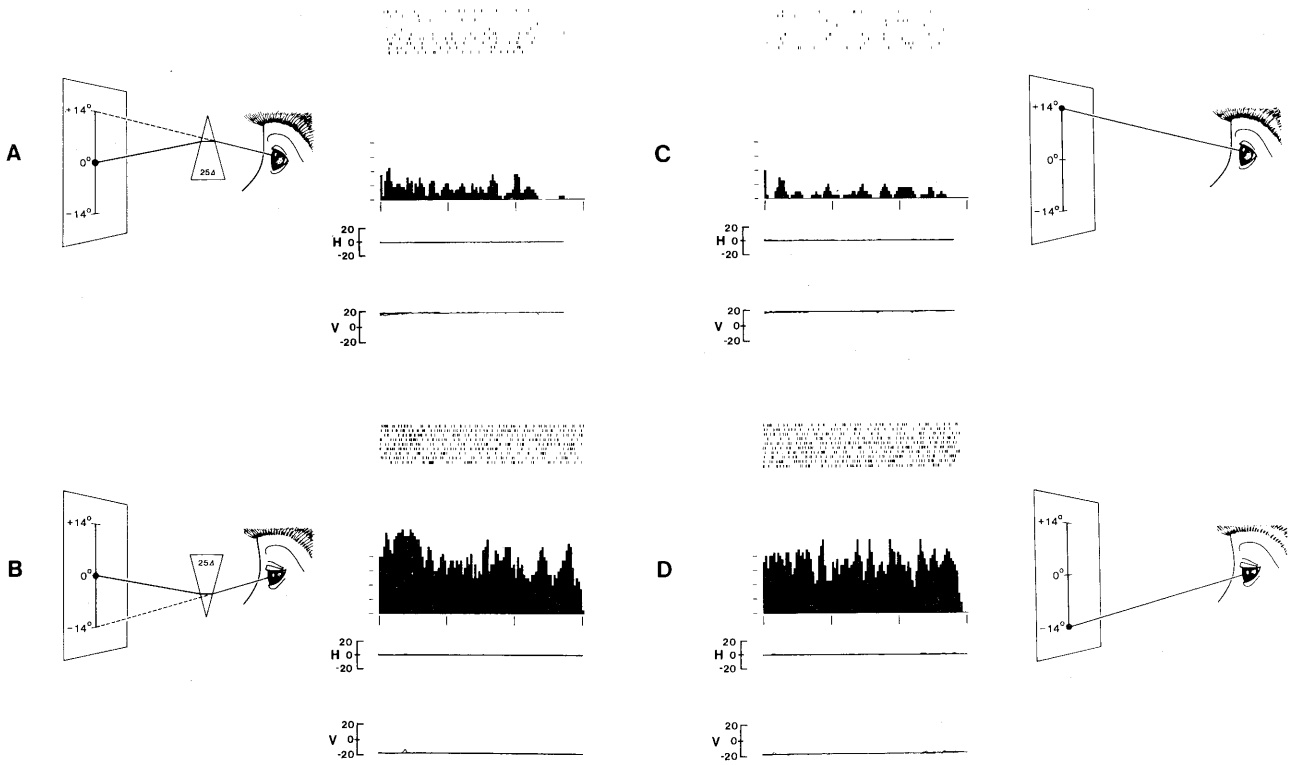

Fig. 1A–D. Task for separating visual and eye-position related activity. In **A** and **B** the animal fixates, with head fixed, a point of light in the center of the screen (0,0) through two 25 diopter prisms. With prisms base down (**A**) he must look 14 degrees up from straight ahead and with base up (**B**) he must look 14 degrees down to fixate the target. In **C** and **D** the prisms are removed and the animal is made to look 14 degrees up (**C**) or 14 degrees down (**D**) by moving the fixation point up or down on the screen. The angles of gaze are the same in **A** and **C** and in **B** and **D**. The retinotopic positions of the visual background are the same in **A** and **B** but different in **C** and **D**. The recording data adjacent to each corresponding schematic indicate that the cell's activity varies with eye position and not with changes in retinotopic locations of the visual background. The spike rasters are synchronized to the animal pulling a key back to begin each trial. The height of each 10 ms bin of the histograms represents the discharge rate at that time, averaged over all the trials in the raster. Vertical 5 spikes/div horizontal 1 s/div. The horizontal (h) and vertical (v) eye position traces are measured in degrees of visual angle

position was recorded using the scleral search coil technique. The animals' heads were fixed in all experiments, and they faced a large featureless back-projection screen subtending 100 degrees horizontally by 125 degrees vertically. An even background illumination of 1 cd/m^2 was used, and the visual stimuli were 1 × 1 or 6 × 6 degree squares 1 log unit above background. The fixation points and saccade targets were 0.25 degrees in diameter. The animals sat in a light-tight chamber that was completely dark when the background lighting was turned off. Further details of the experimental protocol are described in previous publications (Lynch et al. 1977; Andersen and Mountcastle 1983; Motter and Mountcastle 1981).

Results

Fixation activity was assessed by having the animals fixate the fixation target for several seconds at each of nine different locations on the screen; each fixation position was separated by 20 degrees of visual angle horizontally and vertically within a 40 by 40 degree square centered on fixation straight ahead. Fixation neurons have been previously classified as cells which show an increase in activity with the behavior of interested fixation (Mountcastle et al. 1975); however, we have found almost all fixation neurons so classified to change their rate of activity with the gaze angle and thus we will also refer to these neurons as eye-position cells. Of 340 neurons from three hemispheres examined in this task, 173 (51%) showed some modulation of their tonic activity as a function of eye position. One hundred-thirty of these cells showing an eye-position-dependent modulation in activity were analyzed for light sensitivity by flashing the visual test stimulus at various locations in the visual field while the animal fixated the fixation target at the center of the screen. Seventy-one percent of the eye-position neurons were found to have visual receptive fields by this method.

We performed two further experiments on the fixation neurons in order to show that the eye-

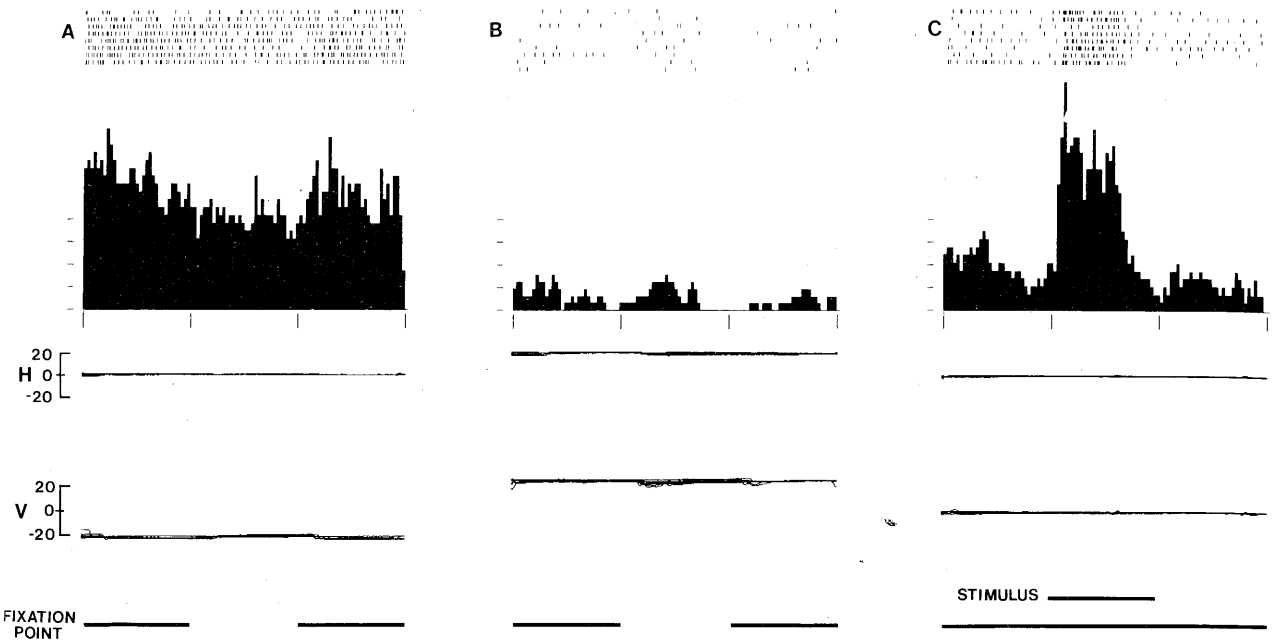

Fig. 2A–C. Second paradigm for separating visual and eye-position responses. **A** The animal fixates a fixation point located 20 degrees down from the center of the screen in otherwise total darkness. The broken line at the bottom of the panel indicates the time that the fixation point was on and off. Note that the eye position traces indicate that the animal did not break fixation when the fixation point was turned off. **B** Same as **A** but with the animal fixating the target up 20 degrees and right 20 degrees. **C** The animal fixates the fixation target, which does not blink on and off, and a second visual test stimulus is flashed in the visual receptive field of the cell evoking a response. Vertical 4 spikes/div; horizontal 1 s/div

position component of the activity was not an artifact of visual stimulation. Such an artifact could arise from the visual background of the experimental chamber stimulating the receptive fields of these cells by varying amounts at the different angles of gaze. In the first experiment the animal fixated a small spot of light on a tangent screen while looking through prisms. When the diopter values of the prisms are changed, the animal must change its angle-of-gaze to maintain foveation of the fixation target, which is not moved on the screen. As a result, the angle of gaze can be changed without significantly altering the retinotopic locations of the contours of the visual background of the recording chamber. The cell illustrated in Fig. 1 is most responsive when the animal fixates 20 degrees down from straight ahead regardless of whether the angle of gaze is changed by changing the prisms (Fig. 1A, B) or by changing the location of the fixation point on the screen (Fig. 1C,D). Thus the tonic activity of the cell is related to the eye position; change in the retinotopic locations of the visual background of the experimental chamber did not appreciably affect this response. Of 12 neurons with fixation responses tested in this way, 11 showed the same eye-position-related activity with or without prisms.

In the second set of experiments, the animal was required to fixate a small spot of light backprojected onto the screen in otherwise total darkness and to maintain fixation at the same location on the screen when the fixation point was turned off for one second. In this condition there are absolutely no visual inputs and any change in activity of the neurons with the angle of gaze must be related to eye position. A typical recording is illustrated in Fig. 2; this cell responded best for fixation 20 degrees down regardless of whether the room lights were off and only the fixation point was on, or whether the fixation point was also turned off and no visual stimuli were present at all. Of 67 neurons we examined in this task, 62 (93%) showed eye position signals in total darkness. Most of these neurons also responded to visual stimuli as illustrated in Fig. 2C.

In the eye movement task the animals fixated a fixation target at the beginning of the trial. After one second of fixation the fixation target was turned off and a second target was simultaneously turned on at a second location on the screen. The animals made a saccadic eye movement to fixate the second target light. Of the 212 neurons that were tested in this task 96 showed a change in activity associated in some way with saccades.

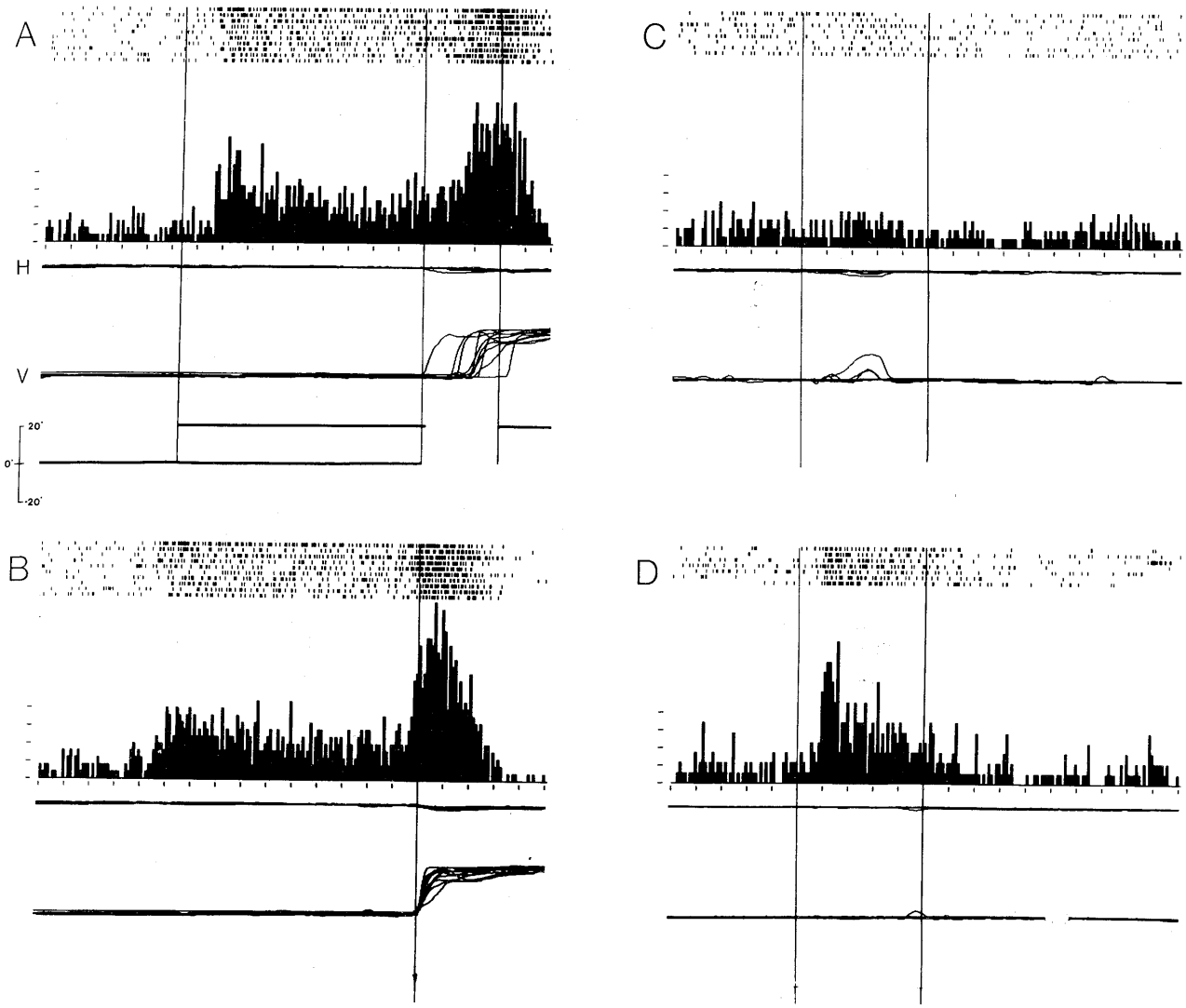

Fig. 3A–D. Task for making saccades to remembered locations in total darkness. **A** The spike rasters and histograms are aligned to the stimulus events which are diagrammed in the lower part of the panel. The first vertical line indicates the time of onset of the saccade target 20 degrees above the fixation point; the second vertical line the time of offset of the fixation target (and 60 ms later the saccade target); and the third line, the reappearance of the saccade target. **B** The spike rasters of panel **A** are now aligned to the beginning of the eye movement, indicated by the vertical line. **C** The same fixation task as in Fig. 2A used as a different control. The first vertical line indicates the time of offset of the fixation target and the second line the time the fixation target came back on. **D** In this fixation task the fixation target remained on throughout the trial. A visual stimulus identical to the saccade target was flashed on (first line) and off (second line) at 20 degrees above the fixation point. Vertical 25 spikes/div, horizontal 100 ms/div

Seventy eight of the 96 cells whose activity changed in the above eye movement task were further tested in a paradigm designed to separate saccade-related responses from visually related responses. Visual responses may arise from stimulation of the cell by the target for the saccade or by the movement of the contours of the visual background across the retinas as the eyes move. In this second saccade task the animals were trained to make eye movements to remembered locations in space in total darkness. Figure 3 illustrates the results of a representative recording experiment. One second after the animal fixated the fixation target a saccade target appeared peripherally. The animal was required to withhold his response for a variable period (averaging 1 s) at which time the fixation light went off, thereby commanding him to make a saccade to the second target. Sixty ms later (and well before the saccades were initiated) the saccade target went off as well, and the animal then made the eye movement in complete darkness to the location where the second target had been. In later experiments the

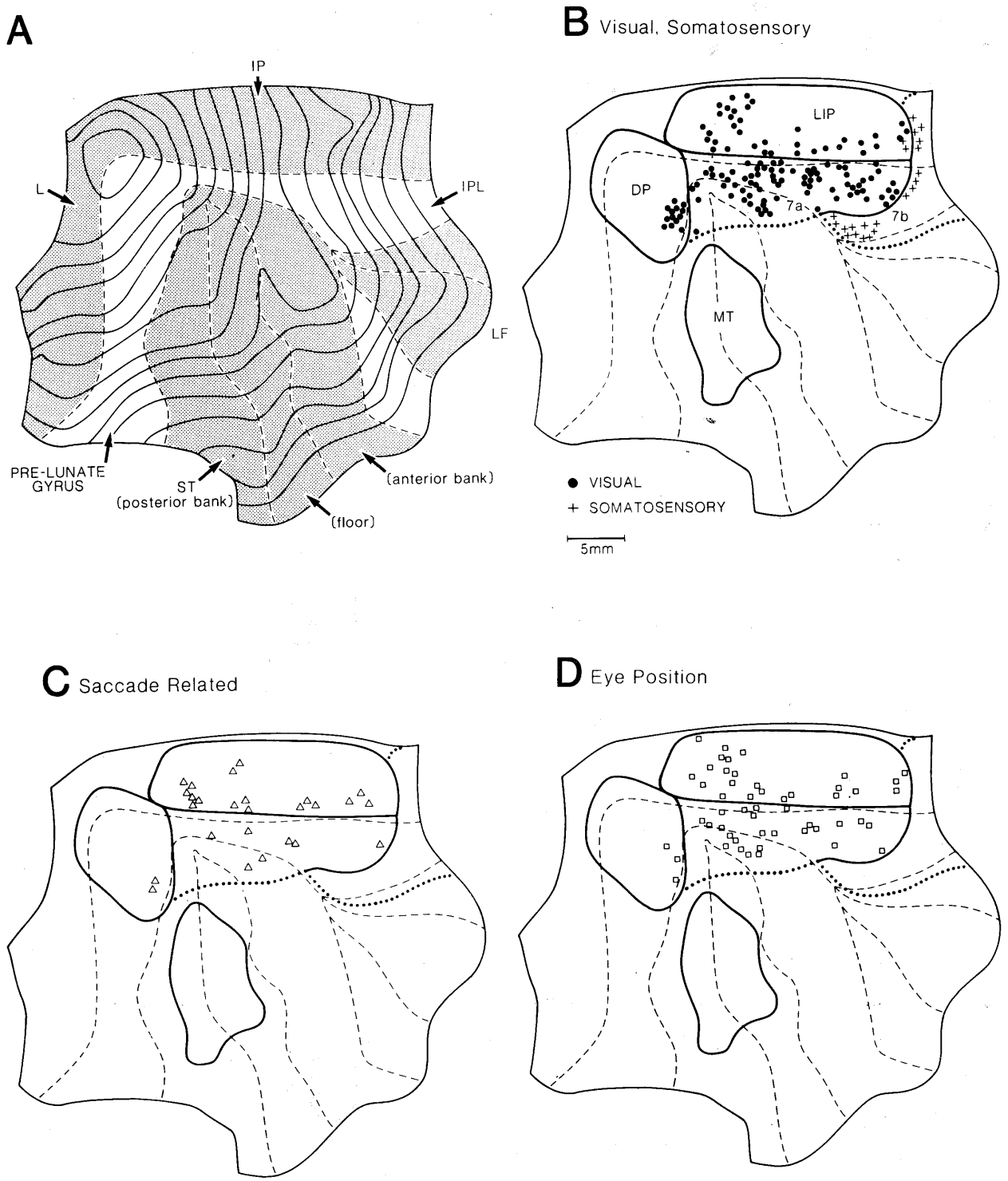

Fig. 4. A Flattened reconstruction of the inferior parietal lobule and dorsal aspect of the prelunate gyrus from one hemisphere of one of the monkeys used in this study. The stippled areas show cortical regions lying buried within sulci. The series of contour-like lines are tracings of layer IV taken from coronal sections through this area that are used in the reconstruction. **B** Location of cells with visual and somatosensory related activity. In the inferior parietal lobule visual cells were found in areas 7a and LIP and somatosensory cells in area 7b. Area MT was identified by its characteristic heavy myelin staining. **C** Location of cells with saccade-related responses. Many of the cells from this hemisphere were located near the border between areas 7a and LIP. Since this border is difficult to determine precisely on cytoarchitectural grounds it is difficult to assign these cells with certainty to either 7a or LIP. **D** Distribution of cells with eye-position-related responses which were found in both areas 7a and LIP. Abbreviation: L, lunate sulcus; IP, intraparietal sulcus; ST, superior temporal sulcus; LF, lateral fissure; DP, dorsal prelunate area; LIP, lateral intraparietal area; MT, middle temporal area

saccade target was flashed on the screen for only 200 ms at the beginning of the trial, 500 to 1500 ms before the primary fixation target was extinguished. As indicated in Fig. 3a, the cells generally showed two responses, one related to the appearance of the saccade target and one to the saccade onset. In Fig. 3b, the same spike rasters are aligned to the beginning of the eye movement rather than to the stimulus events, demonstrating that the second bursts of activity are synchronized to the eye movements and not to the stimulus events. To ensure that the responses were not linked to the offset of the fixation target, we had the animal perform the task of maintaining fixation in total darkness (as outlined above and illustrated in Fig. 2c) and found that the cells did not show an off response after the offset of the fixation point as long as the animal did not make a saccade (Fig. 3c). Likewise there was no off-response to the saccade target when it was turned off and the animal did not make an eye movement (Fig. 3d). Of the 78 cells examined in these tasks 46 were found to have true saccade-related responses; significantly, 37 of these cells were also found to be light sensitive. The remaining 32 neurons did not show saccade-related responses and gave only visual responses. Only 5 of the 46 saccade-related cells had activity that preceded the eye movement. Most of the cells responded at, or just after, the beginning of the eye movement (median latency 75 ms after the beginning of the eye movement).

Figure 4 shows the histological location of the recording sites on a flattened reconstruction of the cortex of the inferior parietal lobule and dorsal aspect of the prelunate gyrus from one of the hemispheres used in this study. All the visual cells were located in the posterior aspect of the inferior parietal lobule, whereas somatosensory and reach-related activity was found more anteriorly on the gyrus. Saccade cells were found in both area 7a on the gyral surface, and lateral intraparietal area (LIP; Andersen et al. 1985a) in the lateral bank of the intraparietal sulcus. In general saccade-related activity in area LIP occurred earlier than for area 7a neurons and all five neurons showing pre-saccadic activity were found in area LIP. Eye position neurons were also found in both areas 7a and LIP.

Discussion

The results of these experiments show conclusively that the fixation and saccade neurons have responses related to both the oculomotor behavior and to visual stimuli. The work of Hyvärinen and colleagues has suggested a convergence of visual and ocular motor signals in the posterior parietal cortex; however, their experiments did not use eye movement recordings which are necessary to establish this convergence with certainty (Hyvärinen and Poranen 1974). Additional evidence for a convergence of visual and oculomotor properties comes from the work of Sakata and colleagues (Sakata et al. 1980; Sakata et al. 1983). They have found that fixation cells in area 7 can be modulated by turning the room lights on and off, and that tracking neurons are also light-sensitive. Since the eye-movement-related response of most of the saccade neurons begins at or after the beginning of the saccade it seems unlikely that these cells play a role in the generation of eye movements. Rather, the saccade-related response probably represents reafference from oculomotor structures or proprioceptive input from the extraocular muscles informing this spatial-perceptual area that an eye movement is occurring. Recently we have found cells in area 7 in which the amplitude of the visual response is modified by the position of the eyes in the orbits (gaze angle) (Andersen and Mountcastle 1983; Andersen et al. 1985b). This interaction results in the eye-position-dependent tuning of neuronal responses for the locations of visual stimuli in at least head-centered coordinates. The eye position signal may be used for the modulation of the visual response of these cells and thus may play a role in encoding the locations of visual stimuli in space. Therefore, both the eye position and eye movement signals could play an important role in establishing or maintaining perceptual stability of space and providing the motor systems with the head- or body-centered coordinates of targets that are necessary for calculating the correct trajectories of eye and limb movements.

Acknowledgements. We thank Drs. W.M. Cowan, F. Crick, and S. LeVay for comments on the manuscript. Supported by NIH grant EY 05522, a McKnight Foundation scholars award to R.A.A., a Sloan Foundation fellowship to R.A.A., and the Clayton Foundation for Research – California Division.

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Received June 13, 1986 / Accepted February 27, 1987