

Research Note

Memory related motor planning activity in posterior parietal cortex of macaque

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Summary. Unit recording studies in the lateral bank of the intraparietal cortex (area LIP) have demonstrated a response property not previously reported in posterior cortex. Studies were performed in the Rhesus monkey during tasks which required saccadic eye movements to remembered target locations in the dark. Neurons were found which remained active during the time period for which the monkey had to withhold eye movements while remembering desired target locations. The activity of the cells was tuned for eye movements of specific direction and amplitude, and it was not necessary for a visual stimulus to fall within the response field. The responses appeared to represent a memory-related motor-planning signal encoding motor error. The relation of the activity to the behavior of the animal suggests that the response represents the intent to make eye movements of specific direction and amplitude.

Key words: Saccade – Parietal cortex – Memory – Monkey – Motor-planning – Oculomotor – Motor error – Intention

Introduction

The posterior parietal cortex of primates is involved in sensorimotor processing in both somatic and visual/oculomotor modalities (Critchley 1953, Mountcastle et al. 1975; Hyvärinen 1982; Lynch 1980; Andersen 1987). Recent studies in our lab have

focused on the visual-motor properties of neurons in the lateral intraparietal area (LIP), a cortical field in the lateral bank of the intraparietal sulcus (Andersen et al. 1987; Gnadt et al. 1986). In the course of these studies we have unexpectedly discovered a response property not previously reported in posterior parietal cortex. These responses were triggered by visual stimuli and maintained their activity for several seconds during tasks which required the monkey to withhold planned eye movements. The activity of the neurons was modulated according to the direction and amplitude of the planned eye movement. Using tasks which temporally and spatially separate visual responses from motor responses, we have shown that the activity was related to the eye movements and can occur in the absence of visual stimuli falling within the response field. These neurons appear to hold in short-term memory the metrics of planned eye movements and thus represent the intention to make specific eye movements. The neurons appear to have similar properties to the 'quasi-visual' (QV) cells of the superior colliculus (Mays and Sparks 1980) and to some cells in the frontal eye fields (Bruce and Goldberg 1985) and prefrontal cortex near the principal sulcus (Goldman-Rakic 1987). The QV cells also had sustained activity to brief visual stimuli during delayed saccade trials, and did not require visual stimuli to fall within their response fields (Mays and Sparks 1980). The frontal cortex cells responded tonically to brief visual stimuli and were suggested to be involved in short-term visual and spatial memory (Bruce and Goldberg 1985; Goldman-Rakic 1987).

Methods

An adult male Rhesus monkey (7.5 kg) was trained to fixate and make eye movements to 0.4° light spots backprojected onto a tangent screen 57 cm in front of the animal. Experiments were

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performed in a completely dark room while the monkey was seated in a primate chair with the head fixed. Eye movements were monitored using the scleral search coil technique (Robinson 1963) and the monkey was given liquid reward for completing the correct sequence of eye movements, as described elsewhere (Andersen et al. 1987). Single unit extracellular recordings were made according to standard techniques using transdural penetrations with a hydraulically sealed microdrive mounted over the parietal cortex. Results were obtained from both hemispheres over a period of 10 months. Recording site locations were reconstructed by interpolation from microdrive coordinates (corrected for shrinkage) compared to histologically verified marking lesions made at known coordinates during the last two weeks of recording and to guide wires placed at the time of sacrifice. Estimates were corrected to conform to the histological sections according to landmarks obtained during recordings, such as transitions from somatosensory responses in area 5 on the medial bank of the intraparietal sulcus and the postcentral gyrus, and from transitions in activity levels and spike forms between gray matter and white matter. Penetrations were made into the dorsomedial extent of the lateral bank of the intraparietal sulcus (area LIP) and the adjacent anterior edge of the convexity of the inferior parietal lobule (area 7a).

The monkey was trained to make eye movements to the remembered location of a flashed visual stimulus, similar to the delayed saccade task of Hikosaka and Wurtz (1983). The monkey learned to fixate one spot of light while a second spot was flashed for 300 ms at an eccentric position. When the fixation spot extinguished 500 to 1600 ms later (pseudorandom presentation), the monkey would saccade to the remembered target location and fixate in the dark for an additional 500 ms. An important aspect of this task is that it temporally separates stimulus-related activity from movement-related activity. Movements were performed in complete darkness thus precluding artifactual visual stimulation during the movements. Additionally, this task is interesting because it necessitated the use of a memory-linked internal representation of visual or motor space. To test for visual responses to the offset of the fixation spot, the monkey was trained to maintain fixation of the fixation spot location for 500 ms while the spot extinguished and then reappeared.

Additionally, the double-saccade task first described by Hallett and Lightstone (1976) and later refined by Mays and Sparks (1980) was used to investigate the sensorimotor and the memory related properties of the cells. The monkey was trained to look from an extinguished fixation spot to a target position defined by a brief (60 ms) light flash and then to return to the original fixation position. Both eye movements were performed in complete darkness since the latency to the first eye movement was longer than the duration of the target light, and the target position for the second movement was the remembered location of the original fixation spot. The task was designed such that a visual stimulus never appeared in the response field of the neuron when the trajectory of the second eye movement corresponded to that cell's preferred direction of response.

Results

The following criteria were used to classify functional types according to their response in the task of making single saccades to remembered visual targets. Cells having a response to the visual cue, which was not sustained throughout the response delay period, were classified as *light sensitive*. Cells having a burst of activity slightly before, during, or slightly after the

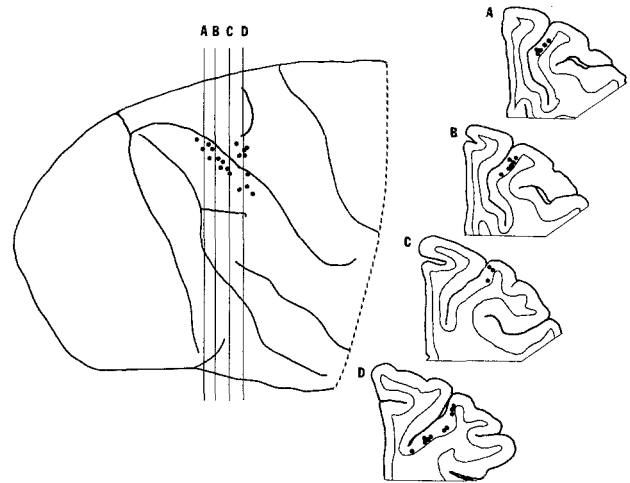


Fig. 1. Recording sites where intended movement cells were encountered. The panel to the left shows the entry points of the penetrations on a drawing of the lateral surface of the macaque brain. Penetrations from both hemispheres have been drawn onto this schematic view from the right hemisphere. Panels A–D show the locations of the recording sites along the lateral bank of the intraparietal sulcus in the representative coronal sections from the positions shown on the drawing to the left. Recording sites have been drawn onto or adjacent to lamina IV, at their estimated locations

eye movement were classified as *saccade-related*. A third class of cells had sustained activity above background during the time period for which the monkey was required to remember the target position but withheld the eye movement. The sustained response of these cells was turned off by the eye movement. For reasons described below, these cells were classified as *intended movement cells*. The data base for this paper is taken from 141 cells recorded from 76 penetrations. Fifty nine cells (42%) were classified as light sensitive, 33 cells (23%) as saccade-related, 10 cells (7%) as light sensitive and saccade-related, and 24 (17%) as intended movement cells. Fifteen cells (11%) were modulated uniquely by gaze direction or other parameters. Twenty five of the 59 light sensitive cells exhibited stronger responses when tested with moving stimuli. Because this sustained responses property was an unexpected finding, systematic searching and testing was not performed until the later stages of the studies. In fact, if not tested explicitly, these cells could appear to be simply light sensitive cells by many routine criteria. They responded phasically and less vigorously to visual stimuli in blocks of visual probe trials that did not require eye movements. For this reason, the proportion of the intended movement cells out of the total is under-represented. This paper will discuss only this new functional class of cells, all of which were located on the lateral bank of the intraparietal

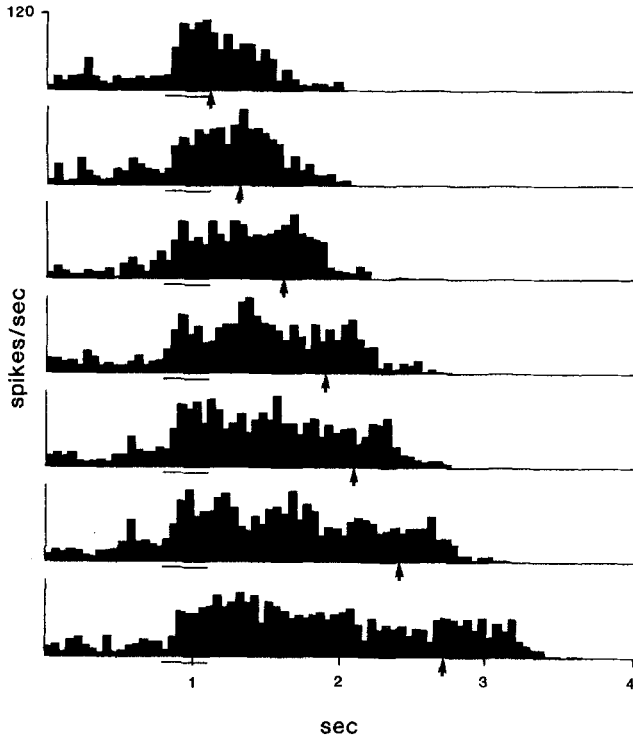


Fig. 2. Spike histograms of an intended movement cell during saccades to a remembered target location within the cell's motor field. Each histogram includes responses for 8–10 trials. Trials are grouped according to increasing response delay times from top to bottom. The horizontal bar below each histogram indicates the stimulus presentation. The arrow indicates the time at which the fixation spot was extinguished. Eye movements occurred from 150 to 400 ms following offset of the spot. Binwidths = 50 ms

sulcus as determined by histological reconstruction of the penetrations (Fig. 1).

Figure 2 shows the response of one of these cells during eight different delay periods. The cell began to respond within 100 ms of the onset of a visual stimulus within its response field. It continued to discharge after the stimulus was extinguished until the eye movement was made, regardless of whether the movement occurred within a few hundred milliseconds or was withheld for more than one and one half seconds. Some of these cells also had either excitatory or inhibitory phasic responses associated with the visual stimulus (2 cells), the saccade (6 cells), or both (7 cells). The beginning of the saccade-related burst for a given cell could either precede or follow the eye movement within a range of 140 ms before to 100 ms after the beginning of the saccade (median = 50 ms before). Interestingly, the QV cells of superior colliculus also often continued to discharge beyond the end of the saccades (Mays and Sparks 1980). The activity during the response delay could be as high as 200–250 spikes/s, sometimes diminishing during the long delays.

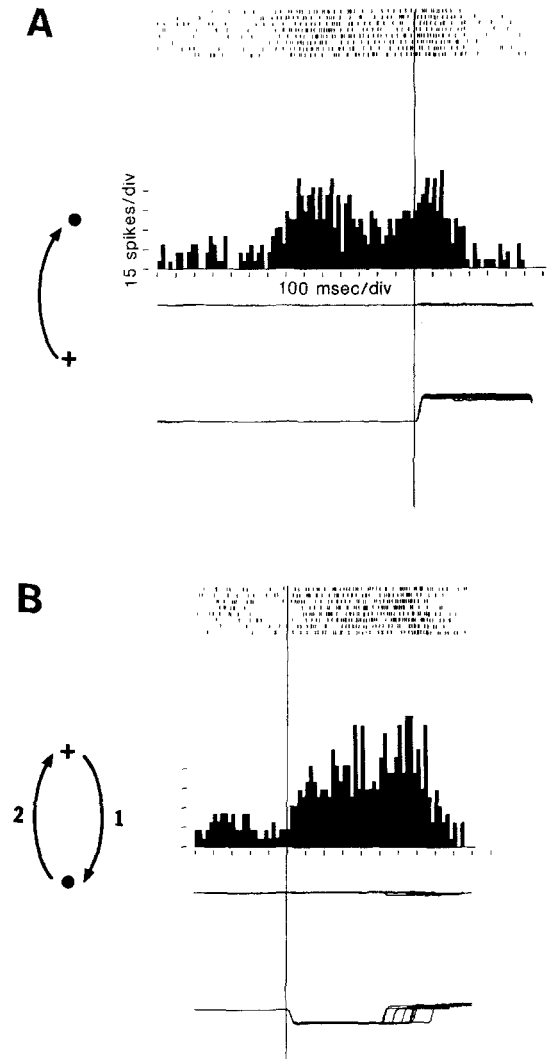


Fig. 3A, B. Motor planning properties of a sustained-response cell. **A** Eye movements straight up into the center of a cell's response field. Trials are aligned to the beginning of the saccade. **B** Double saccade trials with a movement first down then back up into the cell's motor field. Trials are aligned to the first movement. Each panel shows, from top to bottom, the spike rasters for 8 trials, the corresponding histogram with spike rate and time base (binwidths = 50 ms), and horizontal and vertical eye position traces for each trial

The activities of the cells was tuned broadly according to the direction and amplitude of eye movements. Of the 24 cells, twelve were centered in the contralateral direction, eleven near the vertical meridian, and one in the ipsilateral direction. Due to their broad tuning, however, many cells included large portions of both hemifields. Cells having peak activity for 15° eye movements typically had response fields for 50% of peak response of about 90° in direction and 25° visual angle in amplitude. Response fields were smaller for cells tuned for shorter movements, particularly in the amplitude parameter.

Twelve of the 24 intended movement cells were tested in the double saccade task as shown in Fig. 3. This figure shows the response of an intended movement cell with a response field centered approximately 15° straight up. In Fig. 3a, saccades were made to a remembered target location 15° straight up. Trials have been aligned with the beginning of the saccade. The stimulus appeared approximately 800 ms (500 ms delay plus 200–400 ms saccade latency) prior to the beginning of the eye movement. This cell also had a phasic saccade-related burst of activity. Figure 3b shows the response of the same neuron for a sequence of two eye movements: first down to the location of the flashed light, then back up to the remembered location of the extinguished fixation point. The slight hypometria of the second saccades is well within the response field of the cell. Note that the activity of the neuron increased as soon as the monkey achieved the first target and was in a position to make the next saccade into the cell's motor field. The activity ceased after completion of the second movement. Because a visual stimulus never fell within the cell's response field, the activity represents the motor coordinates of direction and amplitude of the pending saccade and not the retinotopic location of a visual stimulus on the retinae.

The activity of this cell appeared to represent the intended trajectory of the impending saccade, holding in register the direction and amplitude until the eye movement was performed, but only for the next intended movement.

Discussion

We have shown that there is memory-linked activity in lateral bank of the intraparietal sulcus which is associated with saccadic eye movements of specific direction and amplitude. The activity can be dissociated from the visual stimuli which guide the eye movements. This observation indicates that the cells were not retaining the stimulus property of retinal position. Quantitative testing during limb or head movements was not performed. However, we have tested many cells in this cortical area for cutaneous receptive fields and for responses to passive movements of the limbs and have never observed somatosensory responses in association with these cells. Furthermore, this cortical field projects to other oculomotor structures, but not to somatomotor structures (Fries 1984; Asanuma et al. 1986; Lynch 1985; Petrides and Pandya 1984; Andersen et al. 1985), and, finally, stimulation in this area has been shown to produce saccadic eye movements (Shibutani et al. 1984). Therefore, these cells' activity

appeared to be related to the pre-movement planning of saccades in a manner which we have chosen to describe as motor intention. The term motor intention, as we use it here, is meant to convey an association between the behavioral event (i.e. saccade) and the neural activity. It is not meant to suggest that this neural signal is necessary and sufficient to produce the eye movement. As has been argued for the QV activity of the superior colliculus (Mays and Sparks 1980), a motor error signal such as this must be combined with a 'trigger' signal to produce a saccade after decisions such as target selection have been made. Indeed, in the occasional trials in which the monkey failed to make the appropriate second eye movement into the cells' response field, the pre-saccadic activity was sporadic and not sustained. Furthermore, during spontaneous movements in the dark, the activities of the cells appeared to be only weakly correlated with the eye movements: occasionally bursting for wrong eye movements or for no movements and often not responding vigorously before appropriate saccades. Quantitative testing using behavioral paradigms which systematically control the behavioral significance and consequence of 'wrong' eye movements and 'spontaneous' eye movements will be necessary to characterize these relationships in detail.

The association of parietal cortex function with movement intention is not without precedent. Hyvärinen (1982) has suggested that the posterior parietal cortex may serve to integrate sensory and intentional factors, and the original 'command hypothesis' proposed by Mountcastle et al. (1975) also engendered some form of motor intention factors. Furthermore, Valenstein et al. (1982) have presented behavioral evidence that the characteristic hemineglect syndrome produced by parietal lesions can be explained as a deficit of movement intention rather than sensory neglect. These investigators trained monkeys to respond manually using the extremity contralateral to a stimulus cue. They found that parietotemporal lesions produced deficits related to reaching with the contralateral arm rather than to responding to the cue on the contralateral side of the body. The intended movement cells exhibit neural activity occurring early in the oculomotor planning process which corresponds to behaviorally defined intention. In terms of control system models, this response is a motor error signal of the impending saccade.

In order to make saccades to remembered target locations, the brain must be able to calculate an intended trajectory based on target position relative to current eye position, and must be able to use either proprioceptive feedback or efference copy of

the eye movement to determine the new eye position at the completion of the movement (Helmholtz 1910; Sperry 1950; von Holst 1954). Note that the 'memory' of the target location could be held in sensory (retinal) coordinates until the time of making the movement or in pre-planned motor (trajectory) coordinates. Our data suggest that, at least for single eye movements, the remembered target locations are coded in area LIP as pre-planned motor trajectories by cells which are not sensory in the usual sense. It is not necessary for visual stimuli to fall within their response fields for the cells to become active.

Making two eye movements to two remembered target positions adds additional demands on the oculomotor system. Two general motor-planning strategies are possible. Either a series of two eye movements must be pre-planned or the system must be able to hold in some sort of spatial register the position of the second target, and must use the new eye position at the end of the first movement to calculate the trajectory of the second movement. Our data do not support the first hypothesis since the activity of these cells do not hold in register the movement trajectories during intervening movements.

The posterior parietal cortex of primates contains neural signals appropriate for the building of spatial maps of visual target space (Andersen et al. 1985), memory-linked motor-planning activity and possible corollary feedback activity of saccades (Andersen et al. 1987; Gnadt et al. 1986). These findings strongly argue that the parietal cortex is intimately involved in the guiding and motor planning of saccadic eye movements.

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