

Eye-Centered, Head-Centered, and Intermediate Coding of Remembered Sound Locations in Area LIP

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SUMMARY AND CONCLUSIONS

1. The lateral intraparietal area (LIP) of the posterior parietal cortex lies within the dorsal cortical stream for spatial vision and processes visual information to plan saccadic eye movements. We investigated how LIP neurons respond when a monkey makes saccades to the remembered location of sound sources in the absence of visual stimulation.

2. Forty-three (36%) of the 118 neurons sampled showed significant auditory triggered activity during the memory period. This figure is similar to the proportion of cells showing visually triggered memory activity.

3. Of the cells showing auditory memory activity, 44% discharged in an eye-centered manner, similar to the way in which LIP cells discharge for visually initiated saccades. Another 33% responded in head-centered coordinates, and the remaining 23% had responses intermediate between the two reference frames.

4. For a substantial number of cells in all three categories, the magnitude of the response was modulated by eye position. Similar orbital "gain fields" had been shown previously for visual saccades.

5. We propose that area LIP is either at the origin of, or participates in, the transformation of auditory signals for oculomotor purposes, and that orbital gains on the discharge are part of this process.

6. Finally, we suggest that, by the level of area LIP, cells are concerned with the abstract quality of where a stimulus is in space, independent of the exact nature of the stimulus.

INTRODUCTION

Early researchers considered the posterior parietal cortex to be a classical association area, important for combining information from the various sensory modalities to form a multimodal representation of space (Critchley 1953; Hyvarinen 1982; Mountcastle et al. 1975). Later investigations generally have focused on the coding of only a single sensory modality, usually vision or touch, within this area. It is currently not well understood how information from the different modalities, which are coded in different coordinate frames, are associated in the posterior parietal cortex. The lateral intraparietal area (LIP) has been postulated to play a role in processing saccadic eye movements. This proposal was based on the findings that the area projected to motor structures involved in processing of saccades and that its cells discharged prior to saccades. Further anatomic experiments (Blatt et al. 1990) showed that area LIP is a classic extrastriate visual area based on its anatomic connections. It receives most of its inputs from other extrastriate areas

such as V2, V3, V4, V3a, and PO and these areas in turn receive input from primary visual cortex. The visual activity of LIP cells has been found to be represented in a retinal reference frame (i.e., attached to the moving eye), but monotonically modulated by both eye and head position (Andersen et al. 1990; Brotchie et al. 1995). The nature of these modulations is consistent with the area containing an implicit representation of space distributed over the neural population. This distributed coding has the attractive feature that eye-, head-, or body-centered coordinates can be extracted from the neural population. The question addressed in this paper is how are auditory signals interface with this distributed representation of visual space in area LIP.

Visually triggered memory activity has been described in area LIP (Barash et al. 1991b; Gnadt and Andersen 1988). Special tasks that dissociate the direction of intended eye movements from sensory stimuli have shown that, for a substantial fraction of LIP cells, this memory activity codes the movement the animal intends to make rather than the stimulus per se. Other experiments have also shown that auditory stimuli will evoke memory activity when the animal plans an eye movement to the remembered sound location (Mazzoni et al. 1993). Jay and Sparks (1984, 1987; superior colliculus) and Russo and Bruce (1994; frontal eye fields) have shown that visual and auditory stimuli are brought into a common eye-centered coordinate frame that is used by these areas to code the motor error required to foveate a target. It is conceivable that area LIP might demonstrate a similar common coordinate frame because it projects to these two oculomotor areas and is involved intimately in processing saccades (Blatt et al. 1990). In addition, LIP already receives eye position signals necessary to match visual and auditory locations (Andersen et al. 1990). In the current study, we tested the effect of different eye positions on the responses of LIP neurons to the remembered locations of sounds. Our goal was to determine the coordinate frame of this auditory-triggered activity. We also wished to determine if the auditory memory activity was modulated by eye position, similar to the modulation found for visual memory activity. Such results would show the state of sensory integration in the posterior parietal cortex and possibly indicate the mechanisms used.

METHODS

Recordings were made from 118 area LIP neurons while a rhesus monkey performed a memory saccade task. In this task, dia-

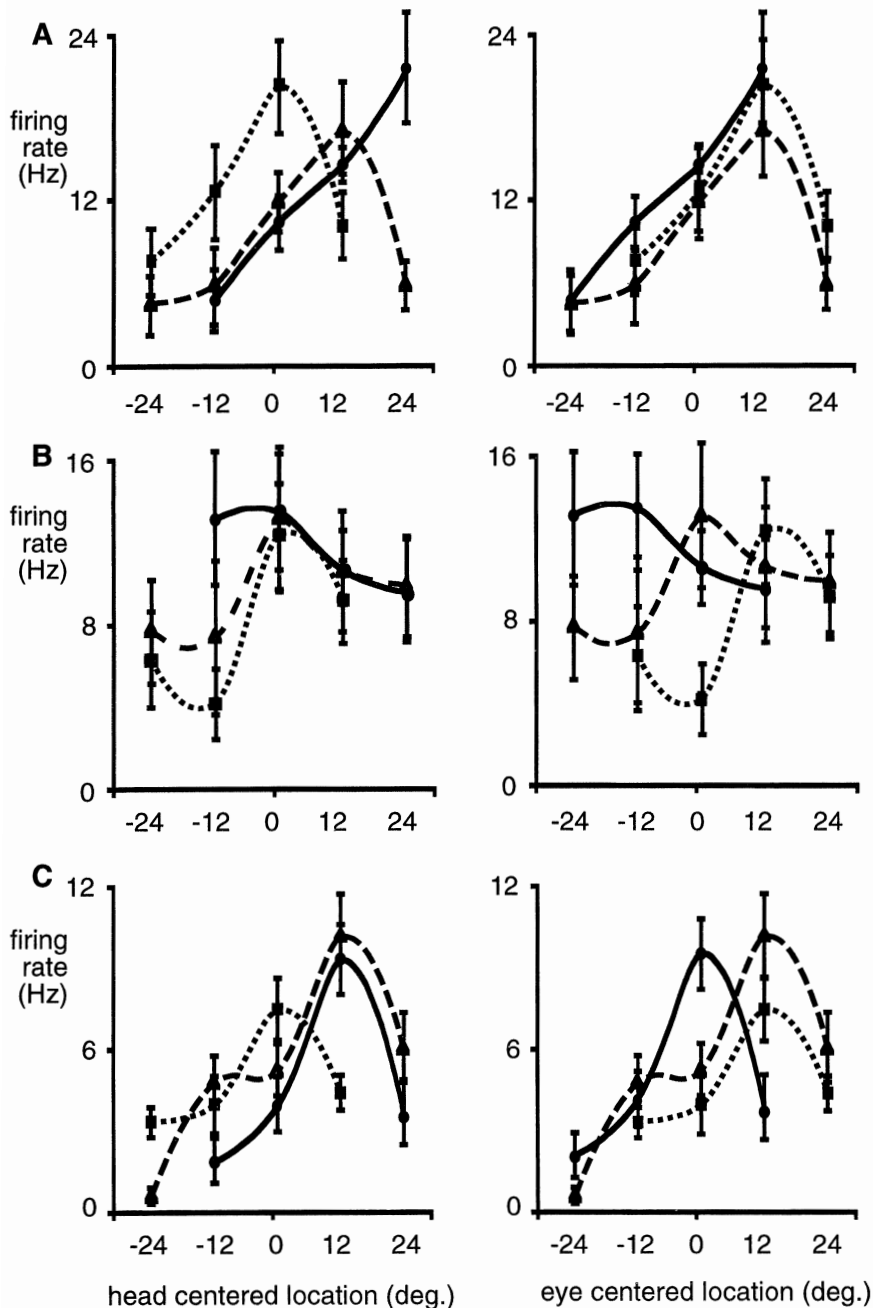


FIG. 2. Tuning curves of 3 representative LIP neurons (A–C). Mean response (averaged over the last 400 ms of delay period, mean \pm SE) is plotted against head-centered location of sound (*left*) or horizontal component of motor error (*right*). Three lines in each plot correspond to neural response obtained from a given starting eye position: 12 deg right fixation, —; central fixation, - - -; 12 deg left fixation, ···. A: neuron with an eye-centered response field: curves obtained for 3 different fixations are aligned on *right*, but not on *left*, showing a strongest response when animal was planning a saccade to a location 12 deg to the right for all 3 fixations (P values: 0.9279 for head-centered location; 0.001 for eye-centered location). B: neuron with a head-centered response field: reverse situation of neuron A, aligned curves on *left* but not *right*, show strongest response for the speaker straight ahead (P values: 0.0468 for head-centered location; 0.3776 for eye-centered location). C: cell with an intermediate response field: here curves are aligned completely on neither plot, but still partially aligned on both (P values: 0.0018 for head-centered location; 0.0138 for eye-centered location).

For all three types of cells, initial eye position can induce a gain on the neural discharge. Figure 3 shows a neuron with an oculocentric response field centered on downward saccades, as indicated by the alignment of the three curves in the motor error plot. However, different starting eye positions significantly modulated the amplitude of the cell's response, resulting in a vertical shift of the curves. A similar gain effect for eye position was seen for cells with response fields in head-centered coordinates and for intermediate cells. The gains were either increasing in the direction of the selectivity (8/16), or in the opposite direction (8/16).

To obtain a more quantitative assessment of the relative distributions of the three types of activity described above, we analyzed the data statistically (see METHODS). Figure 4

shows the distribution of these 43 cells into different categories based on this analysis. Forty-four percent (19/43) of the selective cells respond in oculocentric coordinates ($P < 0.05$ for motor error but not for target location), another 33% (14/43) have head centered response fields ($P < 0.05$ for target location only), and the remaining 23% (10/43) are intermediate cells (significant P values for both variables) (see figure legend).

A second statistical test analyzed the effect of initial eye position on the cell response (see METHODS). For six of the 19 eye-centered cells, 2 of the 14 head-centered cells, and 8 of 10 intermediate cells, the magnitude of the activity was affected by eye position. None of these cells were significant for eye position only, that is, simply coding the position of

centered coordinates through local circuits. This transformation function is suggested by the output of LIP, which projects strongly to both the superior colliculus (SC) and the frontal eye fields (FEF) (Blatt et al. 1990), two areas essential in the programming of saccades (Schiller et al. 1980). Both the SC and the FEF are active in the context of auditory guided saccades (Jay and Sparks 1984, 1987; Russo and Bruce 1994), and both areas have auditory responses in eye-centered coordinates.

Microstimulations of the posterior parietal cortex showed that fixation position influences both the amplitude and direction of the saccades evoked (Kurylo and Skavenski 1991; Thier and Andersen 1991, 1996). Looking at the systematic effect of gaze angle, these studies revealed sites from which the stimulations would evoke saccades of a constant vector and other sites which would bring the eyes to a zone fixed relative to the head. Neural network models of LIP have suggested that the combination of visual information in eye-centered coordinates with eye position signals can form the basis of a implicit representation in head-centered coordinates that would emerge from the activity of the whole population (Mazzoni et al. 1991; Zipser and Andersen 1988). For instance, when a single unit of such a network is stimulated (Goodman and Andersen 1989), it produces, for different starting eye positions, saccades of the same direction, whose amplitudes often vary with initial eye position. However, simultaneous stimulation of an increasing number of units results in saccades that are increasingly more convergent.

We propose that LIP brings auditory signals and visual signals into eye-centered coordinates, but information can still be extracted in other coordinate frames because of the way eye position signals are incorporated. Indeed, a recent neural network model by Xing et al. (1994) studied how information about either visual or auditory cues can be used by the same network to provide areas like the SC or the FEF with a motor error signal. Once trained, the middle layer units in the network had many properties that were similar to what is found in area LIP: for visual saccades, an oculocentric coding modulated by orbital gains; and for auditory saccades, head-centered and intermediate coordinate frames also modulated by orbital gains. When a similar network is trained for both eye- and head-centered outputs simultaneously, these particular cell properties still are found (J. Xing, personal communication).

Finally, we suggest that, by the level of area LIP, cells are concerned with the abstract quality of where a stimulus is in space, independent of the exact nature of the stimulus. Indeed, Maunsell and colleagues recently have shown that many V4 cells are selective for the orientation of a sample stimulus, which could be either tactile or visual, when matched to the orientation of a visual stimulus (Haenny et al. 1988; Maunsell et al. 1991). Possible interpretations they raised were that the activity reflected either the mental image of an oriented visual stimulus being searched for or else an orientation per se independent of sensory modality. Our results would suggest that LIP is concerned with location per se rather than an imagined visual stimulus. Indeed, in our study, the saccades were made in the dark and only to auditory targets; the animal was not required to match the sound to a visual stimulus. Our results and those of Maunsell et al.

suggest that extrastriate areas code abstract representations, rather than simply raw features of the visual scene.

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