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

BRIGITTE STRICANNE, RICHARD A. ANDERSEN, AND PIETRO MAZZONI

Centre de Recherche Cerveau et Cogniscience, Universite Paul Sabatier, Faculte de Medecine de Rangueil, 31 000 Toulouse, France; Division of Biology, California Institute of Technology, Pasadena, California 91125; and Columbia-Presbyterian Medical Center, Department of Psychiatry, New York, New York 10032-2603

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 sacades (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-

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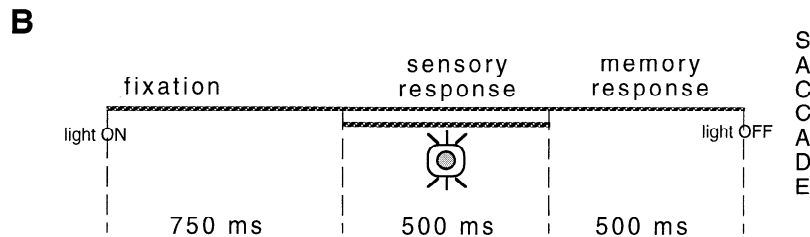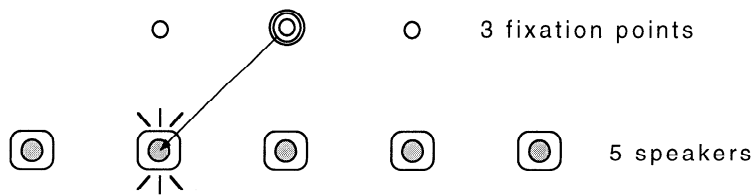auditory delayed saccades from various fixation points

FIG. 1. Schematic representation of the experimental paradigm. Stimulation apparatus (*A*) consists of 5 speakers displaced horizontally, centered straight ahead from the monkey and separated by 12 deg. A round fixation light (0.5 deg; 45 cd/m^2) is back projected on a translucent screen 10 deg above either of 3 central speakers. Auditory stimulus is a white noise burst of 20–20,000 Hz and 70–80 dB. *B*: timing in task: monkey fixates for a total of 1,750 ms; after 1st 750 ms of fixation, a 500-ms noise burst is emitted from 1 speaker; finally, after a delay of 500 ms, the fixation spot extinguishes, and the monkey makes a saccade to the remembered sound location.

grammed in Fig. 1, the animal made saccades to the remembered locations of sound sources from various initial eye positions, with the head fixed and in complete darkness (see figure legend for details). We chose to arrange the speakers only horizontally because horizontal discrimination of sounds is much more accurate than vertical discrimination and memorized saccades are already less accurate than saccades to visible targets (Gnadt et al. 1991). A 12-deg separation between the speakers appeared to be the optimum for the monkey's sound localization ability (~80% correct for an accuracy of 5 deg around the target). This, however, limited saccades to 12 and 24 deg because 36-deg saccades are very unnatural, potentially uncomfortable, and thus likely to decrease substantially the monkey's performance.

We monitored the monkey's eye movements using the scleral search coil technique (Robinson 1963). The animal received a reward of apple juice each time he accomplished the task successfully. Single-cell recordings were made with either glass-coated or insulated tungsten microelectrodes. Each condition of the experimental paradigm was presented between 8 and 12 times, and all conditions were interleaved using a random block design.

We analyzed the cell responses during the delay period, using the mean firing rate during the last 400 ms of this 500-ms time segment. We used a general linear model (a more robust version of the analysis of variance) to test the significance (for *P* values <0.05) of the effect of two discrete variables on cell responses: the horizontal component of the motor error of the saccade (ME) and the head-centered location of the auditory target (HL). A *P* value <0.05 for the variable HL but not for ME means that the response field is stable relative to the head, whereas a significant *P* value only for the variable ME means that the response field moves with the eyes. If, for a given cell, both variables have a *P* value <0.05, it consequently means that this cell has an intermediate response field, which could be fixed relatively to the head for a certain range of stimuli and move with the eyes for another range.

We also tested whether initial orbital position influences the activity through a second general linear model with two discrete variables: the one to which the cell responds selectively (as revealed in the previous test) and starting eye position (EP). When both ME and HL were significant in the first test, we tested the effect of orbital position with each factor separately; conservatively, the *P* value for EP had to be significant in both cases (*P* < 0.05) for the effect to be acknowledged.

RESULTS

During the delay period between offset of the sound and the cue signal to make the eye movement, 43 cells (36%) showed a significant modulation (*P* < 0.05) for one or both of the variables of target location or movement vector. The other cells were either unresponsive during the delay period or, occasionally, were responsive but nonselective for either target location or movement vector. About 75% of these cells had a strong contralateral preference.

Three general cell types were recognized, based on the plots of their response fields; some cells responded in eye-centered coordinates, others responded in head-centered coordinates, and others were intermediate between these two coordinate frames. Figure 2*A* shows an example of a cell coding in eye-centered coordinates. The left plot presents the cell response to different sound source locations. The three curves obtained from three initial eye positions indicate that the cell's response field shifts with different eye positions. The plot on the right shows the same cell's response but now plotted against the motor error of the saccade; the alignment of the curves shows that the shift was equal to the difference in eye position and that this neuron responds most when the animal was planning a saccade to a location 12 deg to the right, independent of starting eye position.

For some neurons, the response to a given sound source does not change when the saccade metrics are changed. These cells code auditory targets invariantly relative to the head. Such a neuron is shown in Fig. 2*B*. The alignments of the three curves in the left plot but not in the right plot show that the cell's auditory receptive field does not change for different eye positions, remaining aligned on the cell's "preferred" sound location (here straight ahead).

A final group of cells appeared to be intermediate between eye- and head-centered coordinate frames. Typically these cells showed only a partial shift of the receptive field with eye position or a shift for two eye positions but not the third. Figure 2*C* shows one particular example of such an intermediate cell; here the three curves are not aligned on either plot.
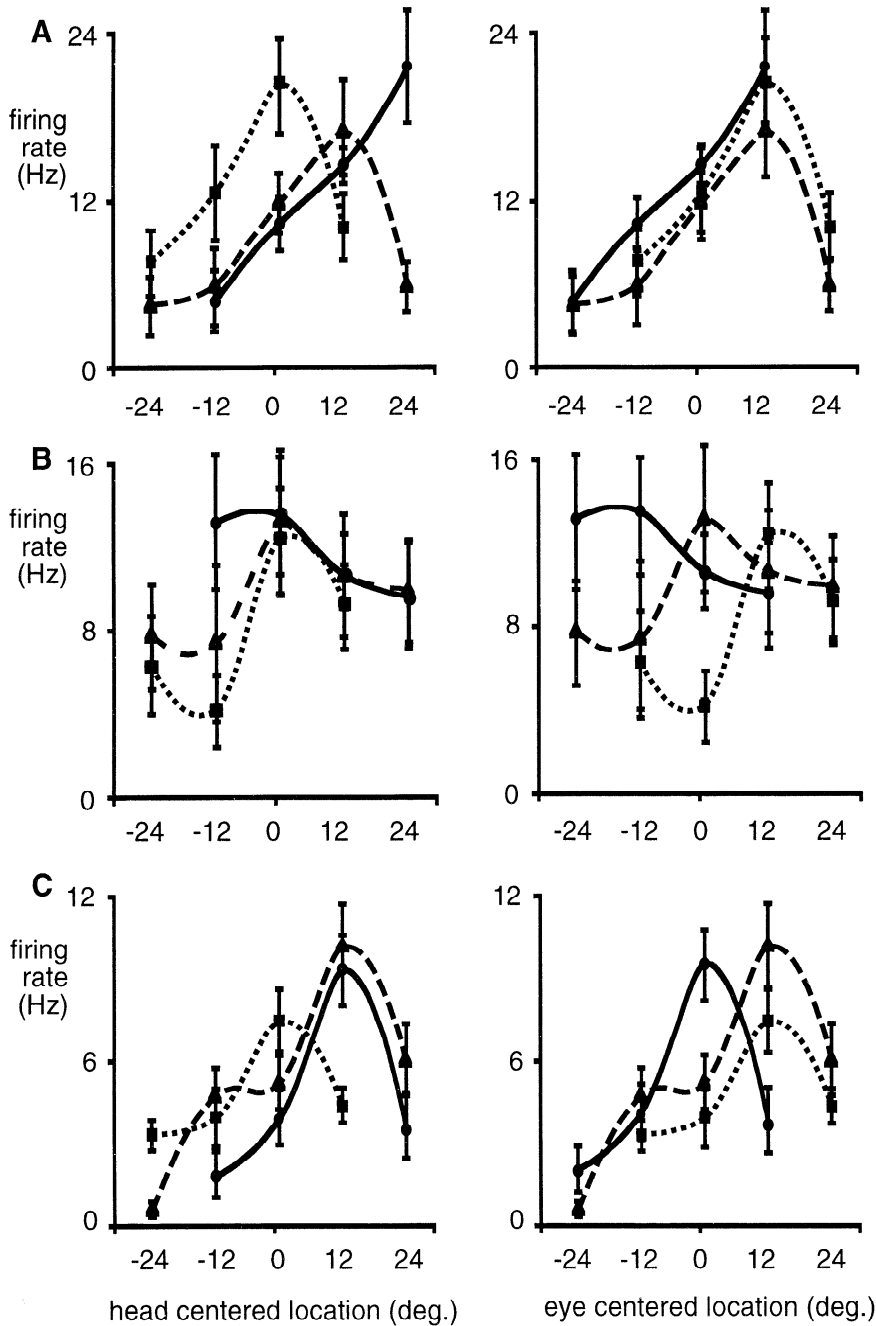
FIG. 2. Tuning curves of 3 representative LIP neurons (*A*–*C*). Mean response (averaged over the last 400 ms of delay period, mean ± SE) is plotted against head-centered location of sound (*left*) or horizontal component of motor error (*right*). Three lines in each plot correspond to neural response 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
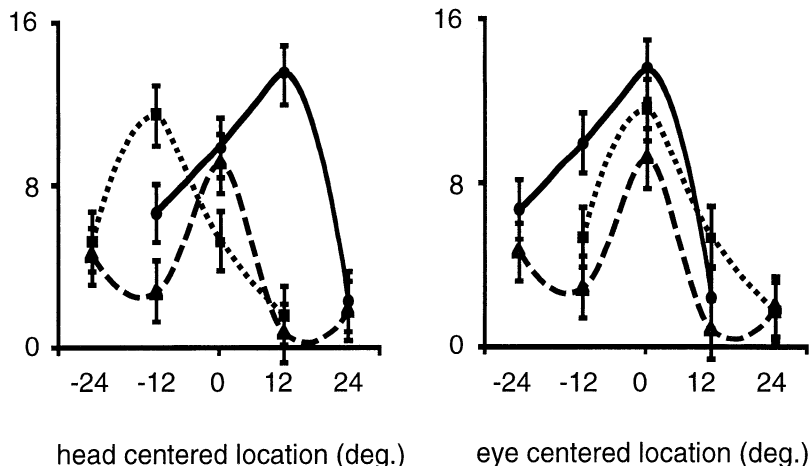
head centered location (deg.)   eye centered location (deg.)

FIG. 3. Neuron with an oculocentric response field modulated by initial eye position (*P* values: 0.2959 for head-centered location; 0.0001 for eye-centered location). Changing initial eye position modulates amplitude of neural response. Indeed, 3 curves are aligned on *right* only, with strongest response for downward saccades for all 3 fixation positions, but intensity of the response is strongest for fixation on *right* (*P* values in second model: 0.0001 for motor error and 0.0050 for starting eye position).

the eyes in the orbits. The relative proportions of cells with these effects are represented in Fig. 4 by the unshaded part of the bars.

Finally, because monkeys can orient their pinnae toward the direction of gaze, different pinnae positions could modify the properties of a given sound entering the ear canals (Bruce et al. 1988). We controlled for pinnae effects by recording while the monkey's ears were taped down tightly. Out of eight cells recorded in this condition, we found one with a head-centered receptive field and three with oculocentric response fields, one of which was also modulated by orbital position. The remaining four cells were not selective during the delay period. The results from this control made it very unlikely that the animal's pinnae orientation would account for the transformation of auditory inputs outlined above.
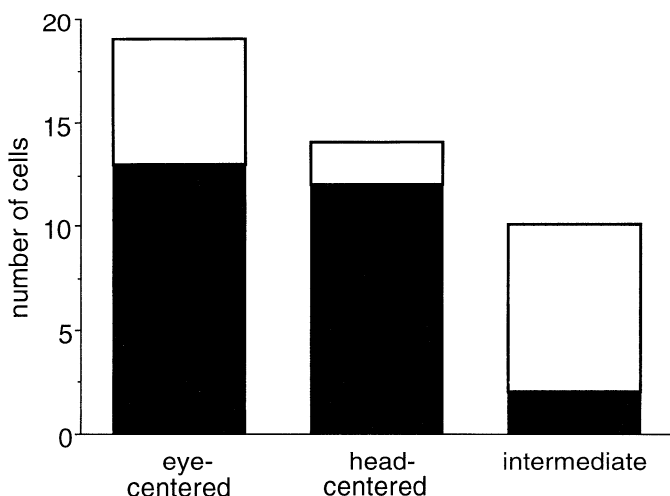

FIG. 4. Population summary, obtained from statistical analysis (general linear model with speaker location and motor error as discrete variables; see METHODS), showing distribution into 3 categories described in text. Because this analysis collapsed data across all 3 eye positions, it tended to average out effects of eye position. A second statistical analysis used starting eye position and factor relevant from 1st analysis as discrete variables. If cell was of intermediate class, then 2 models (1 with motor error and eye position and the other with target location and eye position) were required to be significant for both factors to qualify as a gain effect. Unshaded part of each column shows number of cells in each category for which initial eye position modulates the strength of response.

DISCUSSION

Thirty-six percent of the cells in our sample showed memory activity after presentation of the auditory target. This proportion is similar to the number of cells in LIP showing activity in visual memory saccade tasks (Barash et al. 1991a; Gnadt and Andersen 1988). In this group, we observed both shifts of response fields and modulations of response amplitude with different fixation positions. Amplitude modulations, usually called gain fields, also commonly occur in the coding of visual saccades in LIP (Andersen et al. 1990).

We also found selective responses that occur *during* the presentation of the auditory stimulus. These responses are similarly distributed between the three categories of eye-, head-centered, and intermediate coordinates. However, it is not yet possible to resolve whether this activity is a sensory response or an early elaboration of an activity related to a memory or a plan.

An explicit head-centered coding at the single neuron level in the posterior parietal cortex would appear, at first glance, to be surprising. Numerous studies have shown that visual receptive fields in this region generally code the retinal position of stimuli; an exception has been the report of a few PO neurons, which code in head-centered coordinates (Galletti et al. 1993). The present result is less surprising when considering that the activity is derived from auditory stimuli, which generally are coded in head-centered coordinates. In fact, it is the oculocentric representation of auditory information that is more interesting, because this coding requires a transformation from head- to eye-centered coordinates. We found in LIP both types of representations, plus cells with intermediate coding between the two. This observation suggests that area LIP is either at the origin of, or participates in, the transformation of auditory signals for oculomotor purposes and that this is the functional significance of the co-occurrence of the different cell types.

LIP has very wide response fields that do not appear to be arranged in a strict topography. In addition, eye position influences the response amplitude of cells in each category. The somewhat disordered representation in LIP might be a computational advantage allowing neighboring interactions between cells gated by eye position. These interactions could result in the appropriate transformations from head- to eye-

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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