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Spatially Tuned Auditory Responses in Area LIP of Macaques Performing Delayed Memory Saccades to Acoustic Targets

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SUMMARY AND CONCLUSIONS

1. The lateral intraparietal area (area LIP) of the macaque's posterior parietal cortex (PPC) lies in the dorsal stream of extrastriate visual areas. It receives extensive visual inputs and sends outputs to several eye movement centers. It contains neurons with visual and saccade-related responses suggesting a role of area LIP in programming saccadic eye movements to visual targets. Because primates can also orient to nonvisual stimuli, we investigated whether LIP neurons process stimuli of other modalities besides the visual one by comparing their activity in auditory and visual saccade tasks.

2. We recorded the activity of single neurons of *Macaca mulatta* monkeys while they performed memory saccades to acoustic and visual targets. We analyzed the activity during stimulus presentation (stimulus period, S) and during the delay (memory period, M) between stimulus presentation and the saccade to its remembered location.

3. Among 80 area LIP neurons tested, we found 44 that had S period and/or M period responses following presentation of the auditory stimulus. Most of these responses were spatially tuned, i.e., selective for the left or right stimulus location (27 of 29 S responses; 25 of 29 M responses).

4. The majority of neurons with responses in the auditory memory saccade task also responded in the visual version of the task. Eighty-nine percent (24/27) were clearly bimodal in the S period, and 88% (23/26) were bimodal in the M period.

5. Almost all the neurons with spatially tuned auditory responses that were bimodal were also spatially tuned in their visual responses (20/22 for S responses; 18/19 for M responses). The spatial tuning for the two modalities was the same in 85% (17/20) of the tested neurons for the S responses, and in 83% (15/18) of the tested neurons for the M responses.

6. Area LIP contains a population of neurons that respond to both visual and auditory stimuli. This result is consistent with our finding that the memory activity of many LIP cells encodes the next planned saccade. If cells are coding planned movements, they should be active independently of the sensory modality of the target for the movement, as was the case for most of the neurons described in the present study.

INTRODUCTION

The posterior parietal lobe of the primate brain contains cortical regions that are specialized for localizing visual stimuli (see Andersen 1989 for review). Lesions of this brain region in humans and monkeys produce a range of deficits in the perception of a visual stimulus' location as well as in the programming of orienting and reaching movements toward the stimulus (Balint 1909; Brain 1941; Critchley 1953; De Renzi 1982; Holmes 1918; Lynch 1980, 1992; Lynch and McLaren 1989). For example, one symptom of a bilateral posterior parietal lesion is difficulty in voluntarily shifting gaze from one visual stimulus to another (Balint 1909).

The response properties of posterior parietal neurons suggest that their activity may be the neural substrate for a variety of sensorimotor integration abilities. Recording experiments have recently pointed to an area within the posterior parietal cortex (PPC) [lateral intraparietal area (area LIP)] that may play a special role in programming orienting movements to sensory stimuli. Area LIP was identified as an extrastriate visual area in the occipitoparietal cortical visual pathway, i.e., in the dorsal stream of cortical areas that process mainly the spatial aspects of the visual scene (reviewed in Ungerleider and Mishkin 1982). It receives extensive inputs from several visual areas in the occipital, temporal, and parietal lobes and projects to higher-order visual areas in the parietal lobe, to association and premotor cortical areas in the frontal lobe, and to the intermediate and deep layers of the superior colliculus (Andersen et al. 1990; Blatt et al. 1990; Lynch et al. 1985). Anatomically this area is a link between the early stages of cortical visual processing and premotor, motor, and cognitive centers.

The response properties of LIP neurons also suggest a role in visuomotor processing. When a monkey is trained to memorize the location of a visual stimulus and to look at that remembered location after a delay (memory saccade), LIP neurons modulate their activity selectively for particular stimulus locations and eye movement directions (Andersen et al. 1990, 1992; Barash et al. 1991a,b; Blatt et al. 1990; Gnadt and Andersen 1988). Various proportions of the population of LIP neurons respond during the appearance of the visual stimulus (stimulus period), during the saccade toward that stimulus' location (movement period), and during the delay between stimulus appearance and saccade (memory period). These responses are spatially tuned, that is, the neurons have visual, memory and motor fields, and the three types of fields generally overlap for a given neuron. Gnadt and Andersen (1988) and Barash et al. (1991a,b) hypothesized that these response properties reflect the processing of a sensory stimulus for the programming of a motor plan to orient to that stimulus. Their studies showed that the activity of many LIP neurons encodes the motor coordinates of a saccade to a remembered target not only during the saccade itself but also during the memory period preceding the eye movement. We also later established that the memory-period activity of many LIP neurons reflects the monkey's intention to make a particular saccade (Bracewell et al. 1991; Mazzoni et al. 1992).

The activity of LIP neurons has so far been recorded in tasks that use visual stimuli as cues to spatial locations. Primates can, however, localize stimuli of at least two other

modalities (auditory and somatosensory). We asked therefore whether area LIP is involved in localizing nonvisual stimuli. We recorded the activity of LIP single neurons in monkeys trained to perform memory saccades to auditory targets as well as to visual targets. We found a population of neurons that have spatially tuned activity in the auditory memory saccade task. Most of these neurons responded similarly during the auditory and visual versions of the task.

METHODS

Animals, surgery, and animal care

Two adult male *Macaca mulatta* monkeys were used in this study. Through a surgical procedure a metal head post was mounted in dental acrylic on the monkey's skull, and a scleral search coil was implanted in one eye (Judge et al. 1980; Robinson 1963). The monkeys were trained via operant-reinforcement techniques in several saccade tasks including the ones used for this study. In a second surgical procedure a recording chamber was mounted over the posterior parietal cortex (Brodmann's areas 5 and 7). Several months later a second chamber was mounted over the posterior parietal cortex of the other hemisphere. All surgical procedures were carried out under general anesthesia [10 mg/kg intramuscular ketamine followed by 10 mg/kg intravenous pentobarbital sodium (Nembutal)] using aseptic techniques. After each procedure the monkeys received analgesics and systemic antibiotics and rested for 1 wk.

During the training and recording periods the monkeys had restricted access to water in their home cages and received apple juice or water as reward for correct task execution, supplemented by additional water at the end of each session to reach the required daily ration. Each monkey had at least 2 days of rest per week with unrestricted water access. The monkeys received routine veterinarian care. Their well-being was observed in accordance with National Institutes of Health guidelines.

Experimental setup and behavioral tasks

The monkeys learned to perform several tasks involving saccades for the purposes of several studies. The ones used in this study are the auditory memory saccade task and the visual memory saccade task. The monkey sat in a completely dark room facing a large featureless tangent screen placed 57 cm away. Small light spots (0.5° diam, 45 cd/m^2) were back-projected onto the screen from two projectors through galvanometer-controlled mirrors. A trial started when a spot was turned on directly in front of the monkey and the monkey started fixating on it. After 750 ms a stimulus was then presented for 750 ms to the left or to the right of the fixation spot at an eccentricity of 8°. The monkey had to continue looking at the fixation spot for another 1,250 ms after stimulus offset. At this point the fixation spot was extinguished and the monkey had to make a saccade, in the dark, to the remembered location where the stimulus had appeared. In the auditory memory saccade task the stimulus was a white-noise burst from one of two speakers, each located in front of the tangent screen and 10° to the right or to the left of the fixation point. The speakers' diameter spanned an ~4° angle and produced a relatively uniform sound pressure level between 70 and 80 dB from 20 to 20,000 Hz, with sharp cutoffs to inaudible sound pressure levels (to a human observer) outside this frequency range. In the visual memory saccade task the stimulus was a second light spot that appeared 8° to the left or to the right of the fixation point. We pseudorandomly interleaved left/right and auditory/visual stimulus presentations. A laboratory computer (DEC PDP 11/73) presented the stimuli, monitored the monkey's behavior, and collected eye position and neural activity data.

Data collection and analysis

We recorded eye position with the scleral search coil method (Judge et al. 1980; Robinson 1963), sampling at 500 Hz. We recorded the extracellular potential of single cortical neurons with glass-coated Pt-Ir microelectrodes (Wolshbart et al. 1960) mounted on a Chubbuck microdrive. The laboratory computer stored the eye position samples and the time of occurrence of action potentials for off-line analysis.

We analyzed quantitatively neural activity during three periods of the task defined as follows. For most neurons, the background (B) period was the 450 ms before stimulus appearance while the monkey fixated straight ahead; the stimulus (S) period was from 100 ms after stimulus onset until stimulus offset; and the memory period (M) was from 100 ms after stimulus offset until the fixation point's offset. For several neurons, such a strict definition of the time periods was not appropriate; for example, if a neuron had a phasic burst of activity at the onset of fixation (as described by Mountcastle et al. 1975 for a number of posterior parietal neurons) that overlapped with the initial part of the B period as defined above. The exact starting and ending times of the B, S, and M periods were adjusted manually for these neurons so as to exclude clearly spurious responses.

For each cell we computed a background firing rate B_0 equal to the average firing rate in the background periods preceding left/right auditory/visual stimuli. We defined a response as a significant change in the average firing rate during the S or M periods relative to B_0 (2-tailed t-test, α level 0.05). If a cell had a response in the S or M periods, we considered the response spatially tuned if the response followed only right or left stimulus presentation, or if the response in a left trial was significantly different from the response in a right trial. For cells with clear S-period responses, we estimated the response latency from plots of the firing rate histogram made with 20-ms bins.

Histology

The neurons described in this study were isolated in area LIP of the right hemispheres of two monkeys. After several months of recording the monkeys were killed under general anesthesia with pentobarbital, and the neurons' locations were reconstructed based on each penetrations' chamber coordinates and depth relative to various landmarks. These landmarks consisted of several DC electrolytic lesions made in the last few weeks before death, fluorescent dye injections, and guide wires inserted in the brain before sectioning it (for details see Barash et al. 1991a).

RESULTS

Database

We recorded the activity of 80 neurons in area LIP of 2 hemispheres of 2 monkeys while they performed the auditory and visual memory saccade tasks. Among these neurons we found 44 that had significant responses in the stimulus and/or memory periods of the auditory memory saccade task. These form the database of our study. The remaining 36 neurons responded to visual stimuli at locations other than those of the stimuli used in this study. These neurons were further studied in a separate series of experiments whose results are in preparation.

Stimulus-period responses

We found auditory S responses in 66% (29/44) of the neurons in our database. Figures 1*A* and 2*A* show excitatory S responses to sound from the right speaker. The response

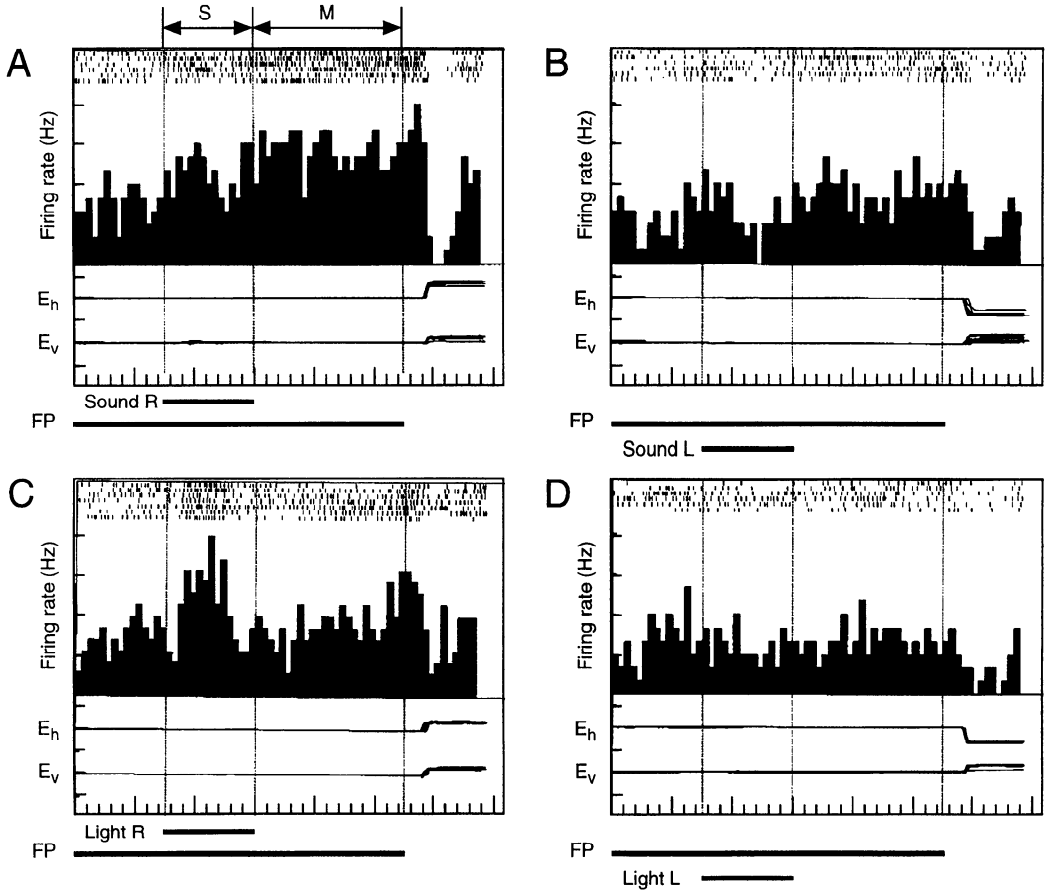

FIG. 1. Activity of a neuron with auditory and visual stimulus (S)-period responses in the auditory and visual memory saccade tasks. In each of the 4 panels, time is plotted on the abscissa. Rows of ticks indicate the occurrences of spikes, 1 row per trial. Below these is a histogram indicating the average firing rate across different trials. The 2 traces below the histogram represent the horizontal (E_h) and vertical (E_v) components of eye position (up represents right, left represents down). The spike rasters, histogram, and eye position traces for each trial are horizontally aligned on stimulus onset. Double arrows above *A* indicate the stimulus (S) and memory (M) periods of the memory saccade task. Thick horizontal lines below each panel indicate the presentations of the stimuli: FP, fixation point; Sound R, right speaker; Sound L, left speaker; Light R, light spot on the right; Light L, light spot presented on the left. *A*: auditory memory saccade to the right. *B*: auditory memory saccade to the left. *C*: visual memory saccade to the right. *D*: visual memory saccade to the left. Scales are 100 ms/horizontal division, 10 (imp/s)/vertical division (firing rate) and 15°/vertical division (eye position).

is absent or inhibitory when the sound comes from the left speaker (Figs. 1*B* and 2*B*), i.e., the response is spatially tuned. The auditory S responses were spatially tuned in 93% (27/29) of these cells.

Most of the cells with auditory S responses that were tested on the visual task also responded to the visual stimulus (89%, 24/27; Fig. 1*C*). In some cells the visual response was larger, whereas in others the auditory response was larger. The onset and time course of the visual and auditory S responses was very similar in some cells and rather different in others (see *Latencies of the S responses* below). The visual S responses were spatially tuned in 88% of these cells (21/24; Fig. 1*C* vs. Fig. 1*D*), and the spatial preference for the visual and auditory stimulus was most frequently the same (85%, 17/20 cells).

The cells without significant visual S responses were not purely auditory; they did have small responses to the visual stimulus that did not reach significance. These responses had the same spatial preference as the auditory ones.

Memory-period responses

We found auditory M responses in 66% (29/44) of the neurons in our database. Figures 1*A* and 2*A* show excitatory M activity after presentation of the sound from the right speaker while the monkey plans a rightward saccade. This activity is absent or inhibited between the left sound presentation and a leftward saccade (Figs. 1*B* and 2*B*). The auditory M responses were spatially tuned in 86% (25/29) of the cells.

Most of the cells with auditory M responses that were tested on the visual task also had visual M activity (88%, 23/26; Fig. 2*C*). As with the S responses, some cells had more M activity in the visual task, whereas others had more M activity in the auditory task. The time course of the M activity in the auditory and visual tasks was very similar in some cells and rather different in others. In almost all cells, however, the activity increased monotonically (or decreased if inhibitory) and remained steady until the fixation point was extinguished. The visual M responses were spatially tuned in 91% of these cells (21/23; Fig. 2*C* vs. Fig. 2*D*), and the spatial preference for the visual and auditory stimulus was the same in most neurons (83%, 15/18 cells).

Of the cells without significant visual M responses, two had some visual M activity that did not reach significance, whereas one had no visual M activity.

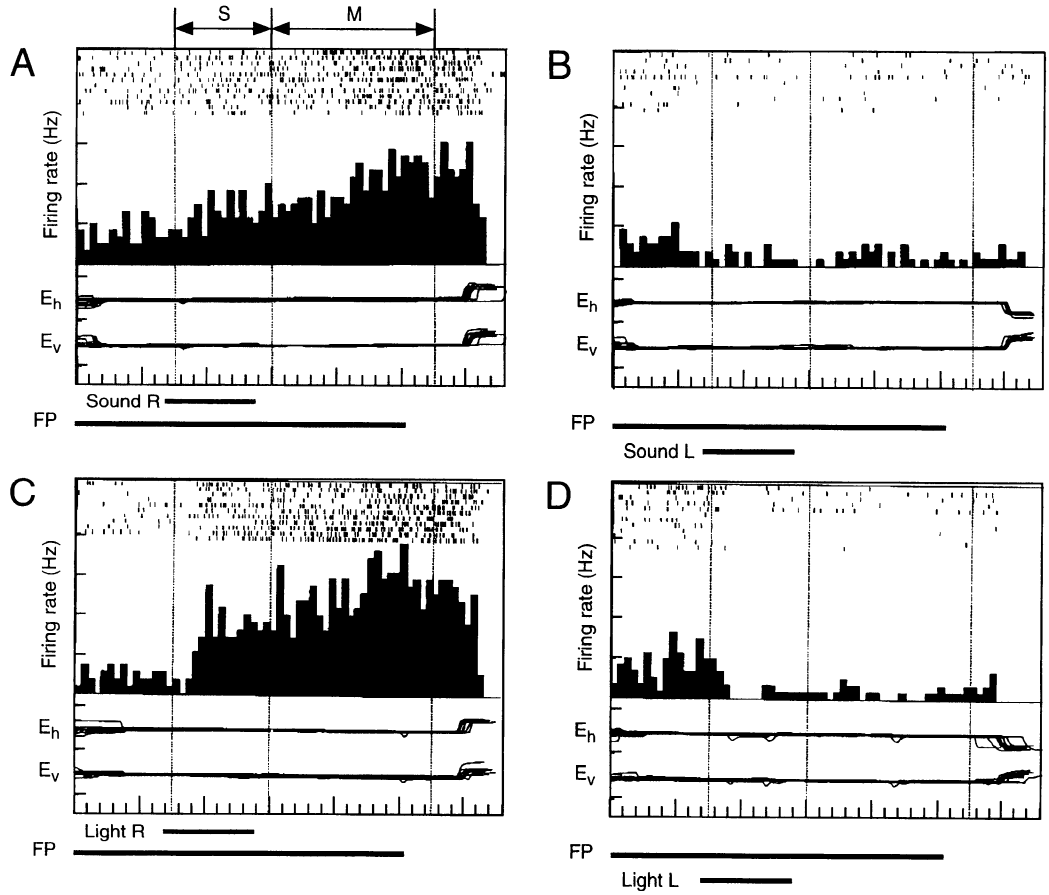

FIG. 2. Activity of a neuron with auditory and visual S-period and memory (M)-period responses. All panels and their labels are as in Fig. 1. *A*: auditory memory saccade to the right. *B*: auditory memory saccade to the left. *C*: visual memory saccade to the right. *D*: visual memory saccade to the left.

Coincidence of auditory S and M responses

Of the 44 cells with auditory S and/or M responses, 41% (18/44) had both S and M, 32% (14/44) had only S, and 27% (12/44) had only M. Compared with the analogous proportions for visual responses reported by Barash et al. (1991a), we found more cells with only M responses (13% in their study) and fewer cells with both S and M responses (58% in their study).

Figure 3 summarizes the distributions within our database of the response properties described so far.

Latencies of the S responses

For a subset of neurons with clear S responses, we measured the latency of S response onset relative to stimulus onset. Latencies of auditory S responses ranged from 30 to 250 ms with a median value of 155 ms (Fig. 4*A*), whereas visual S response latencies ranged from 60 to 210 ms with a median value of 125 ms (Fig. 4*B*). The auditory and visual latencies are thus rather similar across the neuronal population. These values are also similar to the latencies of visual S responses of LIP neurons reported by Barash et al. (1991a).

We also compared auditory and visual latencies within individual cells that had clear S responses to both auditory and visual stimuli. There was no systematic pattern in the differences of latencies, some cells having earlier auditory responses and other cells having earlier visual responses (Fig. 4*C*). The distribution ranged from −90 to 190 ms with median 0 ms.

Saccade-related activity

The majority of LIP neurons we isolated had responses related to the saccade, as was observed by Barash et al. (1991a). Figure 5 shows an example of this activity. Of the neurons with tuned auditory and visual memory responses 73% (11/15) were active during the saccade, the activity always beginning before the saccade. These saccade-related responses all (11/11) had the same spatial tuning for the auditory and visual saccades.

Other response properties

The neurons in this study had excitatory as well as inhibitory responses in the auditory and visual S and M periods. About two-thirds of the responses of all types were excitatory (18/28 auditory S 19/25 visual S, 20/26 auditory M, and 18/28 visual M), and the remainder were inhibitory.

Among the neurons with spatially tuned responses, both contralateral and ipsilateral preferences were represented, but contralateral preferences were more common. Of the excitatory responses, about two-thirds of the S period responses were contralateral (12/18 auditory S, 12/19 visual S), whereas just over one-half of the M responses were

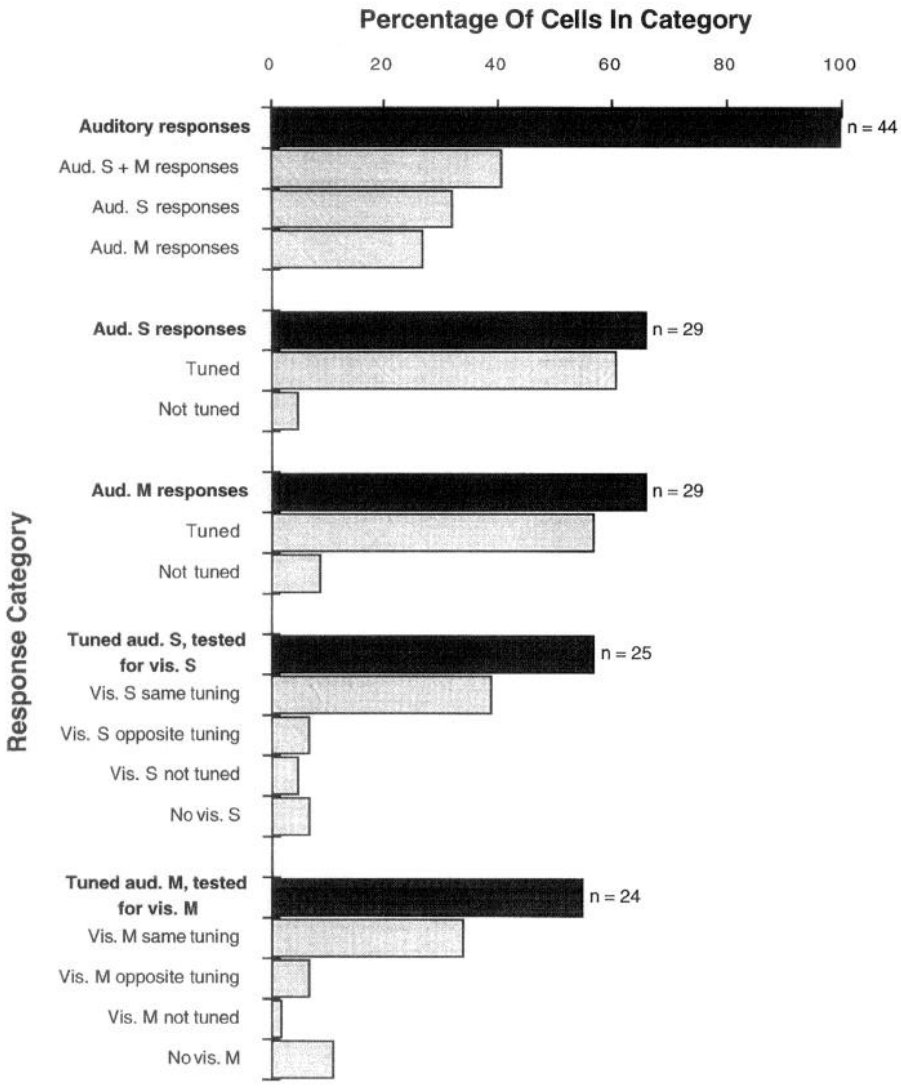

FIG. 3. Proportions of the cells with auditory S- or M-period responses that are in various categories of response types. Each bar shows the number of cells in a response category as a percentage of the cells in our database. Dark bars indicate major response categories, whereas light bars indicate subcategories of the dark bars just above them (the total number of cells in a group of subcategories is the same as the number of cells in the category marked by the dark bar just above them).

contralateral (11/20 auditory M, 10/18 visual M). We report the proportions for excitatory responses for comparison with the percentages reported by Barash et al. (1991b). These are slightly larger for the S responses (71% in their study) and larger for the M responses (69% in their study). The proportions of contralateral and ipsilateral preferences changed only slightly when we included the inhibitory responses: of the spatially tuned responses, 15/28 (54%) auditory S responses and 15/25 (60%) visual S responses were contralateral; 16/26 (62%) auditory M responses and 15/26 (58%) visual M responses were contralateral.

DISCUSSION

Our main findings are that *1*) a population of LIP neurons respond during the stimulus and memory periods of memory saccades to acoustic targets; *2*) most of these neurons respond similarly in the visual memory saccade task; and *3*) the responses of most neurons are spatially tuned, with matching spatial tuning for the auditory and visual modalities.

Stimulus-period responses

A simple interpretation of S responses is that they are sensory responses to a sound in the neurons' auditory receptive fields. This is supported by the fact that they usually start within 200 ms of sound onset, and, in cells without memory activity, they wane before or soon after stimulus offset. They are also almost always accompanied by S responses to visual stimuli. The latter persist in tasks that require no behavior except fixation (Andersen et al. 1985b, 1987; Mountcastle et al. 1975; Robinson et al. 1978) and have thus been considered sensory responses. We did not test LIP responses to auditory stimuli in simple fixation tasks because the monkeys we used were already trained in a number of saccade planning tasks, which made them insufficiently naive for reliable interpretation of results from a fixation task.

These sensory responses could be auditory responses, i.e., arise specifically from the presence of an acoustic stimulus, or supramodal responses, reflecting the presence of a sensory stimulus independently of its modality. The fact that most cells respond to visual as well as auditory stimuli argues for the latter interpretation. The bimodal nature of

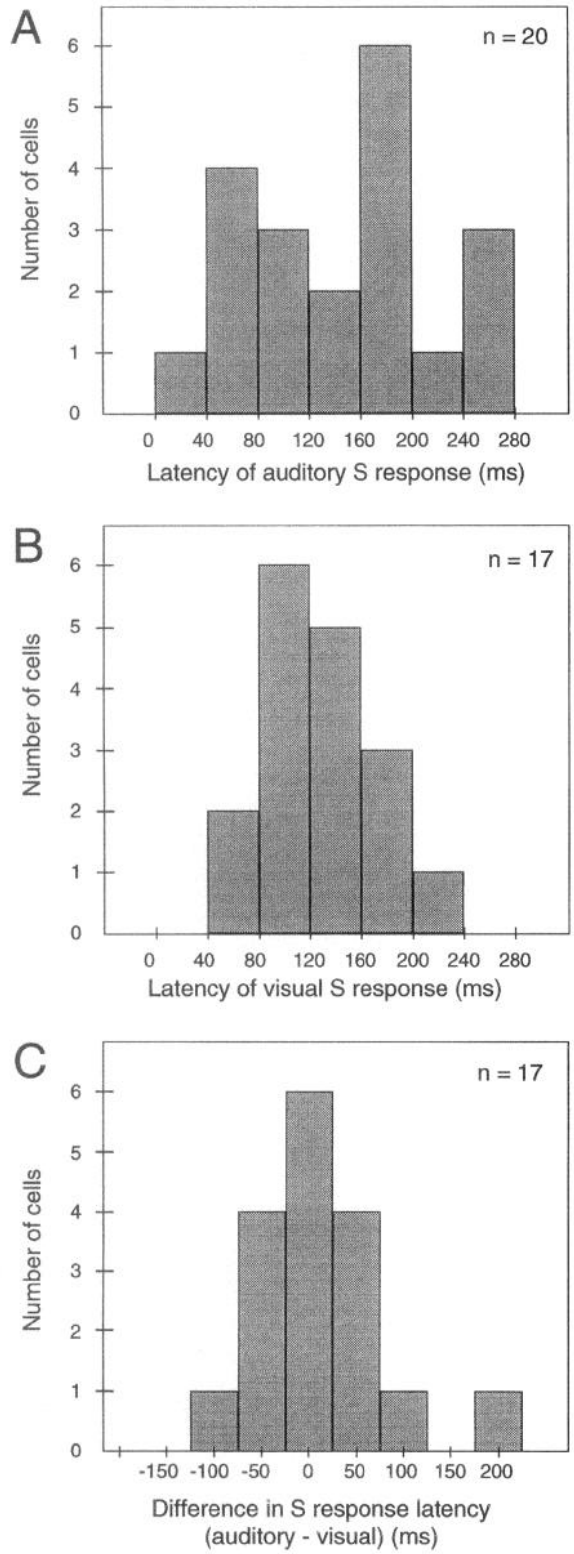

FIG. 4. Latencies of onset of S-period responses of neurons with clear S responses. *A*: latencies of auditory S responses. *B*: latencies of visual S responses. *C*: differences between auditory and visual latencies (auditory − visual) for cells with both auditory and visual clear S responses.

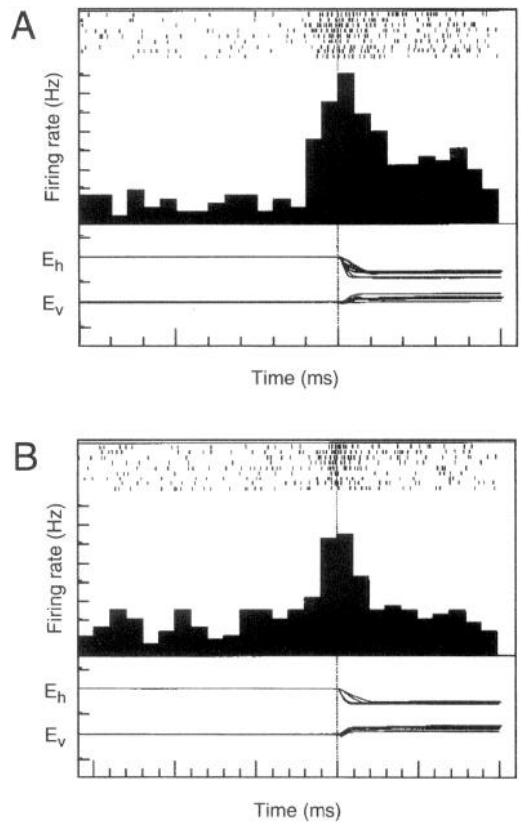

FIG. 5. Activity of a neuron with directionally tuned saccade-related activity during (*A*) a memory saccade cued by the left speaker and (*B*) a memory saccade cued by a light on the left. The spike rasters, firing rate histogram, and eye position are plotted as in Fig. 1, except that all events are horizontally aligned on the beginning of the saccade. Scales are as in Fig. 1.

the responses suggest that the cells are coding spatial location in an abstract manner that is independent of the individual sensory modalities.

Although the latencies of responses to visual and auditory stimuli are often different for an individual LIP neuron, it is remarkable that the median latency difference for all the cells with both auditory and visual sensory responses was 0 ms. This result is in contrast with the response latencies of neurons in primary visual and auditory cortices. V1 neurons tend to have long response latencies (in the range of 25–50 ms) (Maunsell and Gibson 1992) compared with those of primary auditory cortex (~10–12 ms) (Recanzone et al. 1993). The latencies of LIP neurons are also much longer than those of either primary visual or auditory areas, suggesting that significant additional processing time is required between the initial activation of primary sensory areas and the appearance of LIP activity. We know that the shortest connection pathway for visual signals to reach LIP from V1 includes processing in at least two cortical areas (Andersen et al. 1990). The connections from auditory areas to area LIP are less well known, but at least two (and more likely ≥3) cortical areas can be inferred to be interposed between primary auditory cortex and LIP [presuming area Tpt (the temporoparietal junction) to be the major auditory input area to the inferior parietal lobule; see *Anatomic considerations* below]. Thus the additional latency of LIP signals is consistent with known anatomic pathways. The two signals may arrive at similar times in LIP due to a tradeoff of two factors: primary auditory cortex is activated earlier than primary visual cortex, but the auditory signal most likely passes through more cortical areas than visual signals before arriving in LIP.

The absence of a difference in auditory and visual laten-

cies, at the population level for cells with both auditory and visual S activity, suggests that this particular distinction between auditory and visual signals may be discarded in LIP. Neurons with auditory and visual S responses may integrate auditory and visual information into a code that is effectively supramodal and indicates the location of a stimulus independently of its modality. This code could be used, for example, to generate the M-period activity that would in turn be used to program a saccade to the stimulus, as described below.

An alternative interpretation of the S responses is that LIP neurons are purely visual and that their S responses to acoustic stimuli reflect not the auditory stimulus but a visual image of its location. The monkey could in principle localize the speaker's location by imagining its location in a mental visual map, and cells with visual sensitivity could become active as if a visual stimulus had appeared. This would be a very interesting result because it would support certain hypothesized mechanisms of mental imagery (Kosslyn 1988) and because no one has yet reported activity of single visual neurons during mental imagery. Without further evidence addressing this hypothesis directly, however, we prefer the simpler interpretation that the S responses we observed are elicited by the physical stimulus present (the sound) and not by a visual image of it; that is, we consider them auditory responses.

We have referred to the auditory responses we observed as spatially tuned because they were different for sounds coming from speakers at different locations. An alternative interpretation might be that the neurons have some degree of tuning for sound frequency rather than sound location, and that the difference in their responses reflects difference in the frequency spectra of the sounds produced by the two speakers. This possibility seems very unlikely. First, the noise produced by the two speakers did not sound obviously different. We could not discriminate between the two speakers on the basis of their sound quality while sitting in the darkened setup. Moreover, the speaker preference for almost all the bimodal neurons matched their visual receptive field. This result would be quite a coincidence if the speaker preference were due to frequency spectrum tuning. We consider it more likely that these neurons' speaker preference reflects tuning for sound source location. A similar argument can be made to exclude intensity tuning as the source of speaker preference.

In summary, we interpret the S responses as auditory and visual sensory responses that encode the location of auditory and visual stimuli.

Memory-period responses

A group of cells in our study had significant activity during the M period of the auditory and visual versions of the memory saccade task. We refer to these as auditory and visual memory responses, respectively, because in spite of often being very similar they can still be distinguished within each cell by their time course. As for the S responses, we maintain this distinction to indicate that the two activities likely arise from distinct input processes. Also as discussed with regard to the S responses, this still does not exclude that the auditory and visual M responses may play the same role for the two modalities by transmitting the same information (e.g., their average firing rate alone) about the visual and auditory stimuli.

The M period activity could a priori reflect a number of processes. During the delay the monkey must maintain fixation, remember the stimulus' location, shift his attention to that location, and plan a saccade of the appropriate size and direction. The memory activity cannot reflect the maintenance of fixation because it is in general different while the monkey, always fixating straight ahead, remembers and plans saccades to stimuli at different locations.

The hypothesis that the memory activity reflects a shift of visual attention is an interesting one because shifts of attention can indeed modulate the visual responses of PPC neurons (Bushnell et al. 1981) and because attentional deficits are a prominent symptom of parietal lobe damage. The syndrome of unilateral neglect, of which the inability to shift attention while fixating is at least one component (Posner et al. 1984), can include inattention or decreased attention to auditory stimuli in humans (Heilman and Valenstein 1972) and monkeys (De Renzi et al. 1984; Heilman et al. 1971). It is unlikely, however, that the memory activity we observed reflects only an attentional shift. The attentional effects on firing of posterior parietal neurons consist of phasic response bursts (Bushnell et al. 1981), whereas the memory activity of LIP neurons is usually sustained over delays as long as 1,500 ms (Barash et al. 1991a). Moreover, we have shown in a separate study that LIP neurons' memory activity usually does not appear if an attended location, cued by a visual stimulus, is not the target of the next saccade (Bracewell et al. 1991; Mazzoni et al. 1992).

The remaining two hypotheses cannot be distinguished by the results of this study. The memory activity could reflect the monkey's memory of where the stimulus appeared, or it could reflect the plan for the next saccade to be made. In the first instance our results would show that the neurons store bimodal memory traces, or an abstract supramodal memory of a spatial location. If the activity reflects the next saccade's plan, on the other hand, then our findings support the ability of these neurons to generate saccade programs irrespective of stimulus modality. In a separate study in which monkeys made two consecutive memory saccades to locations defined by visual targets (Bracewell et al. 1991; Mazzoni et al. 1992), we have shown that a component of memory activity in area LIP usually reflects the next planned saccade. Moreover, saccade-related activity is present in most neurons with spatially tuned bimodal memory activity (see below). Thus it seems likely that, at least for a certain population of LIP neurons, the auditory and visual memory activity reflects the covert process of programming a saccade to a particular location, regardless of how that location is specified. In other words it is possible that some activity during the S period is not strictly sensory in nature but reflects the animal's intentions to make eye movements. This possibility cannot be determined by the experiments in this study.

Saccade-related responses

A detailed analysis of the saccade-related activity of the neurons in our database was beyond the scope of this study. One relevant result is that many neurons had saccade-related activity, making it likely that we were recording from the same population of neurons as those described in other studies of area LIP (Barash et al. 1991a,b; Thier and Andersen 1991). Barash et al. (1991a) suggested that LIP neurons

with tonic memory activity and presaccadic activity may be involved in the planning of saccades. We found that about three-quarters of the neurons with spatially tuned auditory and visual memory activity also had presaccadic responses in both the auditory and the visual tasks, and these responses had the same spatial tuning independent of the stimulus modality. This result supports a role of the M-period activity in planning the upcoming saccade.

Relationships among signals in different periods

The paradigm used in the present study cannot establish conclusively whether the stimulus-period and memory-period signals have functional roles distinct from each other. Late-starting S activity, for example, could represent early-starting M activity. In fact, because the required saccade is specified uniquely from the moment of stimulus onset, it could be argued that S activity starting at any time could reflect the next planned saccade rather than a purely sensory signal. Indeed, in a related experiment limited to visual stimuli, we found that the stimulus-related responses of LIP neurons can be affected by the monkey's oculomotor plan, suggesting a direct relationship between the S and M signals (Bracewell et al. 1991; Mazzoni et al. 1992). There are neurons, however, with S activity clearly limited to the S period and with no M activity, suggesting that the S activity also plays a "sensory" role by encoding the spatial location of a stimulus.

A complementary possibility is that short-lasting M activity could actually be a prolonged S signal, and that S and M activity is a generalized location signal that is triggered by a sound or light stimulus but that can persist after the stimulus offset. This possibility cannot be excluded conclusively in the present study, but it is unlikely to hold for at least a population of LIP neurons. Experiments cited above (Bracewell et al. 1991; Mazzoni et al. 1992) have demonstrated a certain population of LIP neurons whose M activity is not simply a code of a visual stimulus location but reflects the saccade plan. In those experiments, when the animal was asked to change its planned movement to a new location outside the receptive field, the activity stopped immediately after the cue for the new target location. These cells stopped responding even though the animal made no eye movement at that time. Because the activity was truncated consistently with the change in motor plan, it could not be simply a continuation of a sensory response.

Anatomic considerations

The connections of PPC with auditory areas have not been studied in detail. There are connections from area 22/area TA (areas AA1–3 of Pandya and Yeterian 1985)—the auditory association cortex—to area 7 (both the surface and the inferior bank of the intraparietal sulcus) (Divac et al. 1977). Area Tpt receives connections from parakoniocortex (paAlt) (Pandya and Sanides 1973), considered to be part of the auditory association cortex (Pandya and Yeterian 1985), and projects onto area 7 (Pandya and Kuypers 1969). Leinonen et al. (1980) recorded in this area auditory responses that seemed selective for sound source location. There are also connections from the superior temporal polysensory area of Bruce et al. (1981) to area 7a (Andersen et al. 1990) and LIP (Baizer et al. 1991). Baylis et al. (1987) have reported many auditory responses in single units in the dorsal superior temporal sulcus (areas TS and TAa). Because the various subdivisions of the PPC are densely interconnected (Andersen et al. 1990; Pandya and Seltzer 1982), it seems reasonable to assume that auditory information can gain access to the whole PPC, but indirectly.

Functional role of area LIP

Auditory responses have been described before in the PPC. In early studies, Hyvärinen et al. and Mountcastle et al. (1975) tested several PPC neurons with a few auditory stimuli, such as the jingling of keys and hand clapping, and reported no responses. The neurons tested may have been outside area LIP, which had not yet been identified as a separate area. Various other authors reported auditory responses in portions of PPC (Koch and Fuster 1989; Sakata et al. 1973; Seal et al. 1983). Interestingly, these authors only found responses to auditory stimuli when they were cues for movement. We cannot know whether the same is true for the responses we recorded in LIP because in the task we used the stimulus was always a cue for movement.

Previous recording and lesion studies of area LIP have focused on its role in visually guided tasks. Goldberg et al. (1990; Goldberg and Colby 1992; Goldberg and Robinson 1977; Duhamel et al. 1992) have interpreted the activity of LIP neurons as important for visual sensory and attentional processing. Gnadt and Andersen (1988) and Barash et al. (1991a,b) systematically studied the responses of LIP neurons in monkeys performing visual memory saccades. The responses they observed led them to hypothesize a role for area LIP in sensorimotor integration to guide eye movements. In such a scheme the stimulus-related responses would encode a stimulus' location. The sensory activity would give rise, within the same cells and/or in other cells, to memory activity that would encode the metrics of the upcoming saccade. Saccade centers downstream of LIP could use this signal to generate the appropriate saccade.

Our findings establish that area LIP is not only concerned with processing visual stimuli. We believe we recorded from the same population of neurons as Barash et al. (1991a,b) because we observed response properties in the visual memory saccade task largely similar to the ones they reported (specifically, latencies of the S responses, co-occurrence of S and M responses, proportions of excitatory and inhibitory responses and of contralateral and ipsilateral spatial preferences). Thus area LIP contains a population of neurons that responds to stimuli of at least two modalities. These results extend the possible roles of area LIP in the processing of sensory stimuli. Rather than being restricted to processing retinal events, LIP neurons appear to integrate sensory cues of multiple modalities to encode the spatial location of a relevant stimulus. This integration is consistent with the sensorimotor processing necessary to program orienting movements, regardless of the modality calling for such movements.

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