Responses to Auditory Stimuli in Macaque Lateral Intraparietal Area II. Behavioral Modulation

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Linden, Jennifer F., Alexander Grunewald, and Richard A. Andersen. Responses to auditory stimuli in macaque lateral intraparietal area. II. Behavioral modulation. *J. Neurophysiol.* 82: 343–358, 1999. The lateral intraparietal area (LIP), a region of posterior parietal cortex, was once thought to be unresponsive to auditory stimulation. However, recent reports have indicated that neurons in area LIP respond to auditory stimuli during an auditory-saccade task. To what extent are auditory responses in area LIP dependent on the performance of an auditory-saccade task? To address this question, recordings were made from 160 LIP neurons in two monkeys while the animals performed auditory and visual memory-saccade and fixation tasks. Responses to auditory stimuli were significantly stronger during the memory-saccade task than during the fixation task, whereas responses to visual stimuli were not. Moreover, neurons responsive to auditory stimuli tended also to be visually responsive and to exhibit delay or saccade activity in the memory-saccade task. These results indicate that, in general, auditory responses in area LIP are modulated by behavioral context, are associated with visual responses, and are predictive of delay or saccade activity. Responses to auditory stimuli in area LIP may therefore be best interpreted as supramodal responses, and similar in nature to the delay activity, rather than as modality-specific sensory responses. The apparent link between auditory activity and oculomotor behavior suggests that the behavioral modulation of responses to auditory stimuli in area LIP reflects the selection of auditory stimuli as targets for eye movements.

INTRODUCTION

The process of sensorimotor transformation (conversion of sensory input to motor output) for goal-directed movement presumably involves several steps. At the sensory end of the process, a stimulus is transduced and localized; at the motor end, movement is generated through coordinated muscle activation. Between these two extremes, several other events occur: for example, attention is directed toward the stimulus, the stimulus is recognized as a potential target for movement, a decision to move is made, and the location of the target is transformed from sensory to motor coordinates.

The lateral intraparietal area (LIP), a region of posterior parietal cortex (Andersen et al. 1985), participates in these intermediate stages of sensorimotor transformation. Anatomically, area LIP appears to be involved in conversion of visual input to oculomotor output (Andersen 1987; Colby et al. 1996; Gnadt and Andersen 1988). Located in the middle of the dorsal visual stream, the "where" pathway in vision (Ungerleider and Mishkin 1982), area LIP receives strong visual inputs from multiple extrastriate visual areas and is interconnected with oculomotor centers in the frontal cortex (Andersen et al. 1985, 1990a; Blatt et al. 1990; Stanton et al. 1995), the superior colliculus (Lynch et al. 1985), and the cerebellum (via the pontine nuclei) (May and Andersen 1986).

Like the anatomy, the physiology of LIP suggests that this area links visual processing with oculomotor planning. Neurons in area LIP are activated during visual stimulation (Blatt et al. 1990), during visual attention (Colby et al. 1996; Gottlieb et al. 1998), during eye movement planning (Bracewell et al. 1996; Gnadt and Andersen 1988; Mazzoni et al. 1996b; Platt and Glimcher 1997; Shadlen and Newsome 1996), and during eye movements (Barash et al. 1991a; Hyvärinen 1982; Lynch et al. 1977; Mountcastle et al. 1975). Visual responses in area LIP are spatially tuned in an oculocentric coordinate frame (Barash et al. 1991b; Colby et al. 1995; Gnadt and Andersen 1988) and additionally are modulated by eye position (Andersen et al. 1990b). Neurons in area LIP respond more strongly when the visual stimulus in the receptive field is a saccadic target than when the same stimulus is a visual distractor, even when the offset of the visual distractor is made relevant to the behavioral task (Platt and Glimcher 1997). Moreover, activity in area LIP seems to follow the eye movement plan (Bracewell et al. 1996; Mazzoni et al. 1996b), and LIP neurons respond more strongly to visual stimuli that are targets for eye movements than to visual stimuli that are targets for arm movements (Snyder et al. 1997, 1998). These findings indicate that area LIP plays a special role in directing eye movements to visual stimuli.

Because auditory as well as visual stimuli can serve as targets for eye movements, area LIP could conceivably be involved in auditory-to-oculomotor as well as visual-to-oculomotor transformations. Although the known auditory inputs to LIP are sparse compared with the visual inputs, at least one auditory association area, area 22 and temporoparietal cortex (area Tpt), is linked to the posterior parietal region (Divac et al. 1977; Hyvärinen 1982; Pandya and Kuypers 1969). Polysensory areas in the superior temporal sulcus also project directly to the intraparietal sulcus (Baizer et al. 1991; Blatt et al. 1990; Seltzer and Pandya 1991). Moreover, movement-related auditory responses have been observed in several regions of the brain that are anatomically connected to area LIP, including the frontal eye fields (Russo and Bruce 1994; Vaadia et al. 1986) and the deep layers of the superior colliculus (Jay and Sparks 1987b).

Early physiological investigations of LIP and surrounding regions found no auditory activity in this area (Hyvärinen

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1982; Koch and Fuster 1989; Mountcastle et al. 1975). More recently, however, Mazzoni et al. (1996a) and Stricanne et al. (1996) recorded responses to auditory stimulation in area LIP in the context of an auditory memory-saccade task. Monkeys were trained to remember the location of an auditory stimulus and to make a saccade to the remembered location after a delay. Neurons in area LIP were active not only during the movement and delay phases of this task, but also during the auditory stimulus presentation (Mazzoni et al. 1996a; Stricanne et al. 1996). These recent results, which show that neurons in area LIP respond to auditory stimuli during an auditory-saccade task, seem to contradict the earlier studies, which reported no evidence for activity in area LIP during auditory stimulation.

There are several possible explanations for this apparent discrepancy. One possibility is that neurons that respond to auditory stimulation exist in area LIP but were overlooked in early studies of posterior parietal cortex. A second possibility is that LIP neurons respond to auditory stimuli after auditory-saccade training, regardless of the immediate behavioral context of the auditory stimulation after training. A third possibility is that neurons in area LIP respond to auditory stimuli only when the animal is engaged in an auditory-saccade task. Finally, a fourth possibility is that LIP neurons develop responses to auditory stimuli through auditory-saccade training, and subsequently display auditory activity primarily but not exclusively during an auditory-saccade task. Auditory responses of this type would be affected both by the animal's training history and by the immediate behavioral context in which an auditory stimulus appeared after training.

The companion paper (Grunewald et al. 1999) excludes the first and third of these four possibilities, by demonstrating both that auditory responses do not appear in area LIP before auditory-saccade training, and that auditory responses are observed after training when the animal is just fixating. The present study addresses the second and fourth possibilities, which concern the effects of immediate behavioral context on auditory responses in the trained animal. The experiments show that neurons in area LIP respond more strongly to auditory stimuli when monkeys are engaged in a memory-saccade task than when they are engaged in a fixation task. This behavioral modulation of auditory responses resembles behavioral modulation of delay-period activity. The experiments also reveal that LIP neurons with auditory responses tend to have visual responses, and to exhibit delay or saccade activity. Together, the present study and the companion paper (Grunewald et al. 1999) demonstrate that responses to auditory stimuli in LIP are dependent both on long-term training history and on short-term behavioral context. Furthermore, the results suggest that auditory responses in area LIP are best considered supramodal responses, rather than modality-specific sensory responses. Task-dependent increases in responses to auditory stimuli in area LIP seem to reflect the selection of auditory stimuli as targets for eye movements. Preliminary reports of these results have appeared in abstract form (Grunewald et al. 1997; Linden et al. 1998).

METHODS

Animals, animal care, and surgical procedures

Animals, animal care, and surgical procedures, explained in detail in the companion paper (Grunewald et al. 1999), are summarized only briefly here. Two adult male *Macaca mulatta* monkeys were used as subjects in these experiments. A stainless steel head post, dental acrylic head cap, scleral search coil, and stainless steel recording chamber were implanted in each monkey using standard techniques (Judge et al. 1980; Mountcastle et al. 1975). The recording chamber was mounted normal to the surface of posterior parietal cortex (stereotaxic coordinates at center: 6 mm posterior, 12 mm lateral) over the left hemisphere of *monkey B*, and over the right hemisphere of *monkey Y*. After surgery, monkeys were given at least 1 wk to recover before behavioral training or recording began. All surgical procedures and animal care protocols were approved by the California Institute of Technology Institutional Animal Care and Use Committee and were in accordance with National Institutes of Health guidelines.

Experimental setup

The experimental setup is described in the companion paper (Grunewald et al. 1999). All experiments were conducted in complete darkness, in a double-walled sound-attenuating anechoic chamber (Industrial Acoustics Company). While inside the chamber, the monkey was monitored continuously with an infrared camera and a microphone. The animal faced a fixed stimulus array consisting of a concave rectangular grid of concentrically mounted piezoelectric speakers and light-emitting diodes (LEDs).

Free-field auditory stimuli were 500-ms bursts of band-limited noise (5–10 kHz, 5-ms rise/fall times, 70 dB SPL). This noise band was chosen because macaque monkeys have been reported to localize 5- to 10-kHz bandlimited noise well in azimuth (Brown et al. 1980), and because the frequency responses of the speakers were relatively flat ($\pm$10 dB SPL) within this range. For most of the experiments reported here, the input to each speaker was adjusted to equalize the output amplitude spectrum to $\pm$2 dB SPL within the 5- to 10-kHz frequency band, as measured at the location where the monkey's head would be during an experiment. There were no qualitative differences in behavioral or neurophysiological results obtained before and after the speakers were equalized. Visual stimuli were 500-ms flashes of 70-cd/m^2 red light from the LEDs, each of which subtended 0.4° of visual angle.

The monkey's head was held fixed during all behavioral training and recording sessions. Locations of stimuli are specified relative to the center of the monkey's head, in degrees azimuth right or left of the median sagittal plane and in degrees elevation above or below the visual plane. All stimuli in the concave stimulus array were ~80 cm from the monkey's head.

Behavioral paradigms

Neural recordings were obtained while the monkeys were performing two tasks: the memory-saccade task and the fixation task (Fig. 1). Two fixed stimulus locations were used for all experiments, because the monkeys had great difficulty making accurate saccades to multiple auditory targets, even after months of training. For details on training procedures, see the accompanying paper (Grunewald et al. 1999).

In both tasks, trials began with the appearance of a fixation light, usually directly in front of the monkey at (0°, 0°). [For 2 units recorded in areas that were clearly responsive to downward saccades and to stimuli in the lower hemifield, the fixation light was positioned at (0°, +16°), above the 2 stimulus locations.] The fixation light remained steady after onset in the memory-saccade task, but flashed on and off for 200 ms (and then stayed on) at the beginning of the fixation task. This flash cue was provided to indicate to the animal which type of task he was expected to perform on a given trial. The monkey was required to fixate the central light within 1 s of its appearance and to hold his eye position within a circular window of radius 2–3° centered on that light. After a 1,000- to 1,500-ms interval, an auditory or visual stimulus appeared for 500 ms at one of two possible stimulus locations: left (−16°, +8°) or right (+16°, +8). The

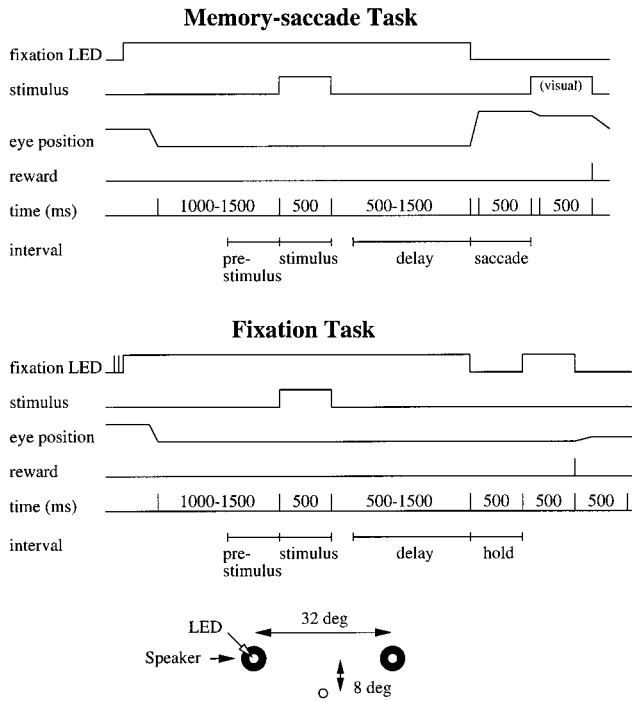

FIG. 1. Time courses for memory-saccade and fixation tasks, and diagram of stimulus array. Schematics for the memory-saccade task (*top*) and fixation task (*middle*) indicate times of trial events in relation to analysis intervals. Cartoon of stimulus array (*bottom*) depicts the relative locations of the fixation light and the 2 auditory/visual stimulus locations. See text for details.

fixation light remained illuminated through this 500-ms stimulus presentation period and through a variable delay period after stimulus offset. For the majority of the experiments, the delay period was 1,000–1,500 ms; in the earliest experiments, a 500- to 1,000-ms or 800- to 1,300-ms delay period was used. The monkey was required to maintain fixation through the stimulus and delay periods in both the memory-saccade and the fixation tasks. Except for the flashing LED at the start of fixation trials, all differences between the two tasks occurred after the fixation light was extinguished.

In the memory-saccade task, the monkey was required to make a saccade within 500 ms after fixation light offset, to bring his eye position into an 8 to 16°-radius window centered 0–6° above the location at which the auditory or visual stimulus had earlier appeared. Eye position window parameters were adjusted within this range for each monkey to accommodate individual variability in memory-saccade trajectories. As previous studies have shown (Gnadt et al. 1991; White et al. 1994), visual memory saccades display a characteristic upshift and are far more variable in endpoint than visually guided saccades. Auditory memory saccades recorded in the present study showed comparable upshift and endpoint variability but were slightly larger in total amplitude (and, for *monkey B*, slower in both latency and peak speed) than visual memory saccades made under identical behavioral conditions.

After completing a memory saccade, the monkey was required to hold his eyes within the eye position window for 500 ms. Then an LED was illuminated at the true target location. To complete the memory-saccade trial and receive a reward, the monkey was required to make a corrective saccade to this visual stimulus within 100–250 ms and to hold his eye position for 500 ms within a 4°-radius window centered on the visual stimulus.

In the fixation task, the monkey was required to continue fixating straight ahead in total darkness after fixation light offset. The animal had to keep his eye position steady for 500 ms within a 4°-radius window centered on the fixation point. Then the fixation light was reilluminated. The monkey's eye position was required to be within a 2 to 3°-radius window around the fixation light within 50 ms of its reappearance; after holding his eye position steady on the reilluminated fixation light for 500 ms, the animal received a reward. The time course of the fixation task was therefore very similar to the time course of the memory-saccade task, except that the animal was required to hold fixation, not to make a saccade, when the fixation light was extinguished. Eye position was recorded for at least 500 ms after the reward, so that very late saccadic eye movements could be monitored.

All behavioral requirements, including eye position window parameters, were identical for auditory and visual trials of the same task. Moreover, auditory and visual stimulus presentations at the left and right stimulus locations were always interleaved (and presented in a balanced pseudorandom order, so that each of the 4 trial conditions appeared at least once in every set of 10 successful trials for each task). The monkey was rewarded with a drop of water or juice for fulfilling all of the behavioral conditions in a given trial. The success rate for memory-saccade trials was usually 80–90%. The success rate for fixation trials was usually >90%.

Recording procedures

Details of the recording procedures are described in the accompanying paper (Grunewald et al. 1999). Briefly, single-unit extracellular recording was performed using tungsten microelectrodes, and all penetrations were approximately normal to the gyral surface. To help ensure that recordings came from area LIP (within the intraparietal sulcus) rather than area 7a (on the gyrus), the electrode was advanced to 2,500–3,000 μm below the dura at the start of each recording session.

Monkeys performed the auditory and visual memory-saccade tasks described above while the recording electrode was advanced in search of neurons. Once a neuron had been isolated, data were collected during a complete block (~10 trials per condition) of interleaved auditory and visual memory-saccade trials. In each trial, an auditory or visual stimulus appeared at one of the two possible stimulus locations, (−16°, +8°) or (+16°, +8°); locations of auditory and visual stimuli were not optimized for the cell's receptive field. If the neuron seemed (by visual inspection of responses) to show modulation of its response in any period of either the auditory or the visual memory-saccade task, data collection continued with a block of interleaved auditory and visual fixation trials, during which stimuli were presented at the same two locations. Memory-saccade trial blocks were alternated with fixation trial blocks for as long as the isolation could be maintained. Typically, one or two blocks were recorded for each task, with about 10 trials per condition in each block.

Eye position was monitored using the scleral search coil technique (Judge et al. 1980) and was recorded at 1,000 samples/s. At the start of each behavioral training or recording session, the animal was required to fixate visual stimuli at each of the stimulus locations used in the experiment, and eye position recording equipment was calibrated.

Analysis

Unless noted otherwise, analyses are conducted on data pooled across monkeys; all significant results for pooled data are significant in data for the first monkey (*monkey B*) alone, and either significant or evident as a consistent trend in data for the second monkey (*monkey Y*, from whom fewer cells were recorded). Because pooled data combine recordings made from different hemispheres in the two monkeys, stimulus locations are identified throughout the text as contralateral or ipsilateral, relative to the hemisphere in which recordings were made. All analyses involve comparison of mean firing rates between contralateral trials (trials involving contralateral stimulus

presentations) and ipsilateral trials (trials involving ipsilateral stimulus presentations). Only differences between contralateral and ipsilateral trials are analyzed, because changes in firing rate that are equivalent for contralateral and ipsilateral trials cannot be distinguished from general arousal effects. However, the trends discussed in this paper persist when such nonspecific responses are also considered.

Neural responses are analyzed in four different intervals: the prestimulus period (the 500-ms interval before auditory or visual stimulus onset), the stimulus period (the 500-ms interval from stimulus onset to stimulus offset), the delay period (the 300- to 1,300-ms interval extending from 200 ms after stimulus offset to fixation offset), and the saccade/hold period (the 500- to 800-ms interval from fixation offset to onset of the corrective visual cue). Note that the animal's behavior during the prestimulus, stimulus, and delay periods was identical in the memory-saccade and fixation tasks. During the saccade/hold period, the animal either made a saccade (in the memory-saccade task) or held his eye position steady without a fixation point (in the fixation task). All analyses are based on correctly completed trials from neural recordings that included at least one block of memory-saccade trials and at least one block of fixation trials.

Analyses of response differentials in a given period involve, for each neuron in the population, calculation of the difference between the mean firing rate in that period during contralateral trials and the mean firing rate during ipsilateral trials. The response differential is therefore the component of the neuron's response that varies with stimulus location, a measure of spatial tuning. An individual neuron has a significant spatially tuned response (or a significant response differential) in a given period if there is a significant difference in mean firing rate between contralateral and ipsilateral trials during that period (Mann-Whitney test, significance level 0.05).

Throughout the text, firing rates and response differentials are expressed in spikes per second (Hz), and nonparametric analysis methods are used wherever possible. All statistical tests are two tailed, and the critical significance level is 0.05 (n.s. means "not significant at the 0.05 significance level"). Applications of bootstrap methods involve 1,000 iterations; in each iteration, a new bootstrap data set is constructed from the original data set by sampling with replacement.

Histology

Electrolytic lesions were placed at two penetration sites in *monkey B* at the end of these experiments. Histological reconstruction of these lesion sites, described in the companion paper (Grunewald et al. 1999), indicated that the electrode penetrations were made in the lateral bank of the intraparietal sulcus. *Monkey Y* is still a subject in ongoing experiments.

RESULTS

Database

The database consists of 160 unit recordings (99 neurons from *monkey B*, left hemisphere; 61 neurons from *monkey Y*, right hemisphere) for which data were collected during at least one block of memory-saccade trials and one block of fixation trials. As explained in METHODS, the animals performed blocks of memory-saccade trials and blocks of fixation trials in alternation during each recording, for as long as the neuronal isolation seemed stable. Most of the recordings (134 neurons) include equal numbers of memory-saccade and fixation blocks (79 neurons, 1 block of each task; 54 neurons, 2 blocks of each task; 1 neuron, 3 blocks of each task). The remaining few recordings (26 neurons) ended after the second memory-saccade trial block and therefore include two memory-saccade blocks and one fixation block. Auditory and visual (and contralateral and ipsilateral) trials were interleaved within each task block.

Behavioral modulation: stimulus period

Many neurons recorded in area LIP responded more strongly to auditory stimuli during the memory-saccade task than during the fixation task. Figure 2 displays the activity of an LIP neuron during presentations of auditory stimuli at the contralateral and ipsilateral stimulus locations, in the memory-saccade task and in the fixation task. Like many other neurons in the database, this neuron has a spatially tuned auditory response; the contralateral auditory stimulus evokes significantly stronger firing than the ipsilateral auditory stimulus in both tasks (Mann-Whitney test on mean firing rates in the stimulus period: memory-saccade task, $P < 0.001$; fixation task, $P < 0.05$). Moreover, like other neurons in the database, this cell is more strongly activated by auditory stimuli in the memory-saccade task than in the fixation task.

In contrast, many visually responsive neurons recorded in area LIP responded similarly in the memory-saccade and fixation tasks. Figure 3 shows the activity of an LIP neuron during presentations of visual stimuli. This neuron has a spatially tuned visual response in both tasks; the mean firing rate in the stimulus period is significantly higher for contralateral trials than for ipsilateral trials (Mann-Whitney test, $P < 0.001$ for both tasks). However, unlike the spatially tuned auditory response of the neuron in Fig. 2, the spatially tuned visual response of this cell appears almost equally strong in the memory-saccade and fixation tasks.

Behavioral modulation of auditory and visual responses across the population is illustrated in Fig. 4. The four plots in this figure show response differentials (differences in mean firing rate between contralateral and ipsilateral trials) for the fixation task plotted against response differentials for the memory-saccade task, for the stimulus and prestimulus periods of both auditory and visual trials. All 160 neurons in the database are included in this figure, so that an unbiased estimate of behavioral modulation across the population can be obtained; because many of the neurons have no spatially tuned response (because stimulus locations were not optimized for each cell), a large cluster appears near the origin in all four plots. Behavioral modulation is assessed in two ways for the data in each plot. First, the number of neurons for which the absolute value of the response differential is greater in the memory-saccade task than in the fixation task is compared with the number of neurons for which the reverse is true. (Absolute values of response differentials are used for this categorization so that excitatory and inhibitory responses are treated similarly.) Binomial test results printed on each plot indicate the significance level for rejection of the null hypothesis that equal numbers of neurons fall into the two categories; $P < 0.05$ implies significant behavioral modulation of response differentials across the population. Second, the two-dimensional least-mean-squares linear fit to the data (line minimizing sum of squared perpendicular distances to data points, i.e., direction of greatest variance in the data) is determined, and 95% confidence intervals on the slope of this line are calculated using a bootstrap technique. The shaded area in each plot indicates the extent of the 95% confidence intervals. (Note that because the confidence intervals are determined through a bootstrap procedure,

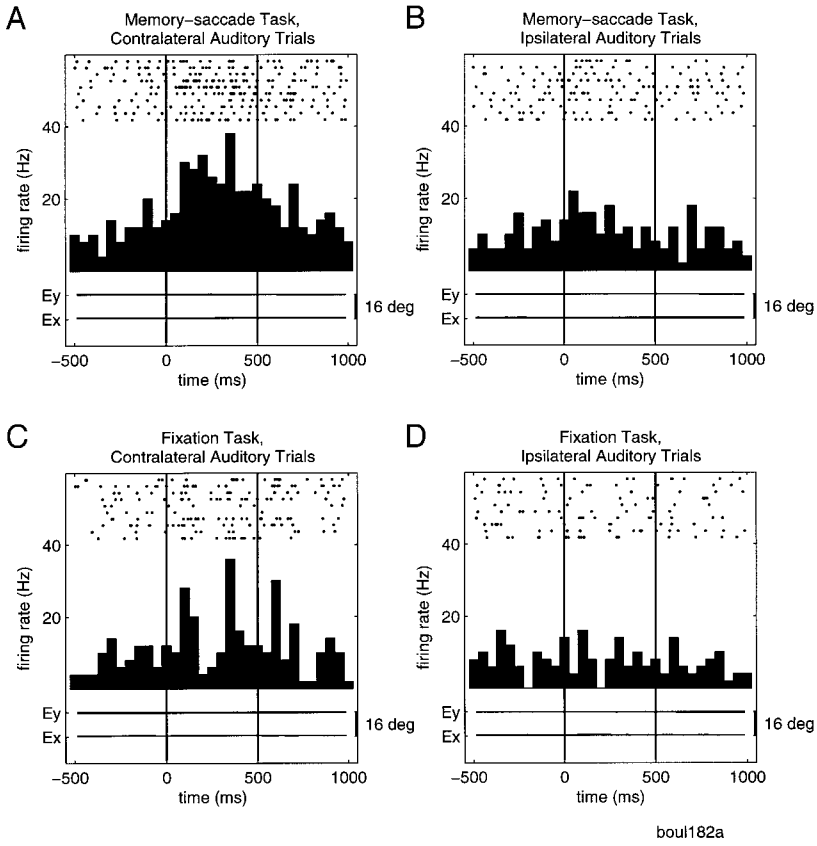

FIG. 2. Activity of a lateral intraparietal area (LIP) neuron during presentations of auditory stimuli. Each plot shows neural activity from 500 ms before stimulus onset to 500 ms after stimulus offset; plot ends before the saccade in the memory-saccade task. The 2 vertical lines in each plot bracket the stimulus presentation interval. Rasters at the *top* of each plot indicate the times of spike occurrence in each trial; histograms show the firing rate of the neuron in spikes/s (Hz) as a function of time relative to stimulus onset; and eye position traces indicate horizontal (Ex) and vertical (Ey) eye position during each trial. *A* and *B*: neural activity during the memory-saccade task, for trials in which an auditory stimulus was presented at the stimulus location contralateral (*A*) or ipsilateral (*B*) to the recording chamber. *C* and *D*: neural activity during the fixation task, contralateral (*C*) or ipsilateral (*D*) auditory trials. The neuron has a significant spatially tuned auditory response in both tasks (Mann-Whitney test: memory-saccade task $P < 0.001$, fixation task $P < 0.05$), but the response differential is larger in the memory-saccade task than in the fixation task (response differentials: memory-saccade task 12.5 Hz, fixation task 6.5 Hz).

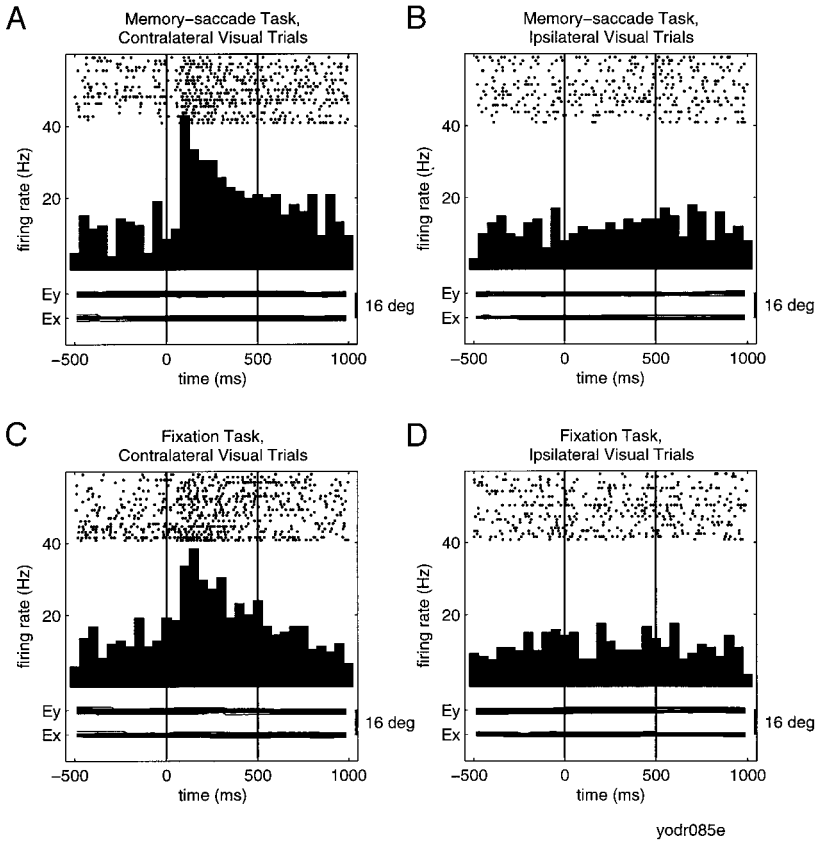

FIG. 3. Activity of an LIP neuron during presentations of visual stimuli. Conventions are the same as in Fig. 2. *A* and *B*: neural activity during the memory-saccade task, for all trials in which a visual stimulus was presented at the contralateral (*A*) or ipsilateral (*B*) stimulus location. *C* and *D*: neural activity during the fixation task, contralateral (*C*) or ipsilateral (*D*) visual trials. The visual response of this neuron is spatially tuned (Mann-Whitney test, $P < 0.001$ for both tasks) and very similar in the 2 tasks (response differentials: memory-saccade task 13.4 Hz, fixation task 13.9 Hz).

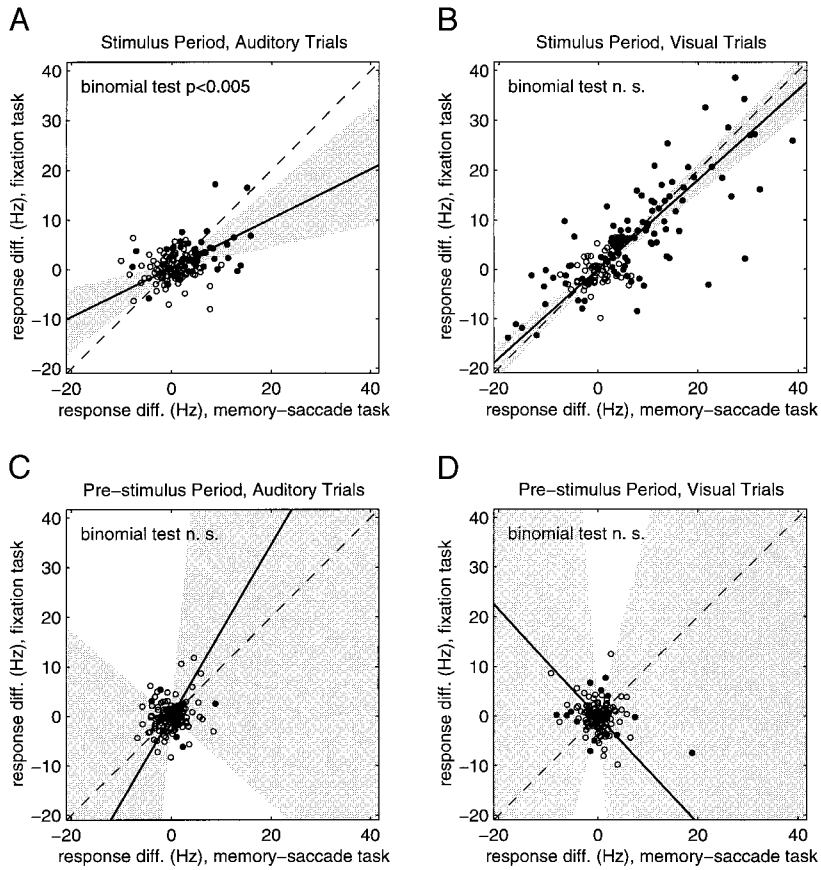

FIG. 4. Effects of behavioral task on spatial tuning in the stimulus and prestimulus periods. Each panel shows the response differential (mean contralateral response minus mean ipsilateral response) in the fixation task plotted against the response differential in the memory-saccade task, for all 160 neurons recorded in both tasks. ●, cells with a significant response differential in at least 1 of the 2 tasks; ○, cells for which neither response differential is significant. Binomial test results indicate the probability that the observed distribution of response differentials might have occurred by chance, if response differentials were not modulated by task. Solid line in each plot is the 2-dimensional least-mean-squares linear fit to the data; the dotted line represents unity slope (no behavioral modulation). Ninety-five percent confidence intervals on the slope, calculated using a bootstrap technique, are indicated in gray. *A* and *B*: response differentials in the stimulus period are significantly modulated by behavioral task for auditory trials (*A*), but not for visual trials (*B*). *C* and *D*: response differentials in the prestimulus (background) period are not affected by behavioral task for either auditory (*C*) or visual (*D*) trials. Slopes of the best-fit lines, and 95% confidence intervals on the slopes: *A*, 0.50 [0.22 0.81]; *B*, 0.90 [0.77 1.04]; *C*, 1.73 [−0.88 10.30]; *D*, −1.08 [−12.43 3.94].

they are not constrained to be angularly symmetrical around the best-fit line.) If the response differential in the memory-saccade task were equivalent to the response differential in the fixation task for each cell, then the slope of the linear fit would be one; this hypothesis can be rejected if the 95% confidence intervals on the slope of the best-fit line do not include one.

These analyses reveal that responses to auditory stimuli are modulated by behavioral task. Across the population, stimulus-period response differentials for auditory trials (Fig. 4*A*) are significantly larger in magnitude during the memory-saccade task than during the fixation task (binomial test, $P < 0.005$; slope of best-fit line significantly less than 1). In contrast, stimulus-period response differentials for visual trials (Fig. 4*B*) are not significantly different in the memory-saccade task and the fixation task (binomial test n.s.; slope of best-fit line not significantly different from 1). Behavioral modulation of visual responses is therefore weak or nonexistent. (Some evidence for weak behavioral modulation of visual responses does exist in the data; although behavioral modulation of visual responses is not significant for either monkey individually according to the binomial test, the slope of the best-fit line is significantly below 1 for *monkey Y*.) For comparison, response differentials in the prestimulus period are presented in Fig. 4, *C* and *D*. The prestimulus period response differentials are not significantly modulated by task during either auditory or visual trials (binomial tests n.s.; slopes not significantly different from 1).

The data in Fig. 4*A* cover a smaller range than the data in Fig. 4*B*, indicating that response differentials in the stimulus period are generally weaker during auditory trials than during visual trials. Could this difference in spatial tuning strength account for the apparent behavioral modulation of responses to auditory but not visual stimuli? If weakly tuned responses were modulated by task, but strongly tuned responses were not, then the analyses would indicate much more behavioral modulation for auditory than for visual responses. According to this explanation for the apparent behavioral modulation of auditory responses, weakly tuned visual responses should also be modulated by task. Figure 5, which is analogous to Fig. 4*B*, shows data from the 134 neurons with weak stimulus-period spatial tuning during visual trials. Neurons included in this plot have visual stimulus-period response differentials that are within the observed range of auditory stimulus-period response differentials (−10.1–17.2 Hz). Even for these weakly tuned neurons, no behavioral modulation of visual responses can be detected (binomial test n.s.; slope not significantly different from 1 in pooled data, or in each monkey's data individually). Behavioral modulation is therefore not a necessary consequence of weak spatial tuning.

These results suggest that behavioral modulation might be a distinctive characteristic of auditory responses. Another possibility, however, is that behavioral modulation might be a characteristic of auditory cells, rather than of auditory responses. In other words, the apparent behavioral modulation of auditory responses might be occurring within a small subpopulation of cells for which visual responses are also modulated by task. To address this possibility, behavioral modulation during the stimulus period was analyzed exclusively for the subpopulation of 45 auditory cells: cells that have significant spatially

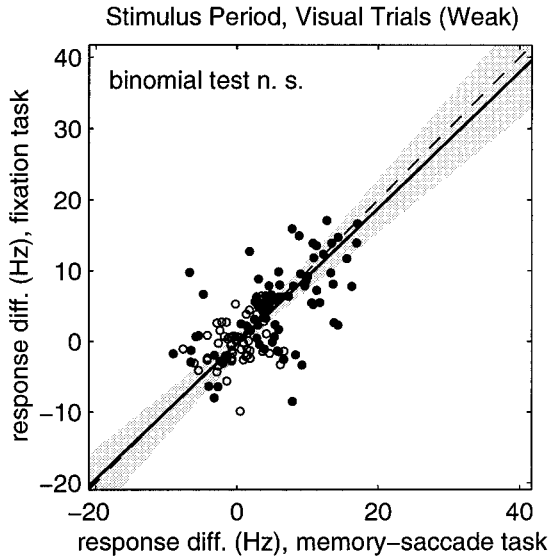

FIG. 5. Effects of behavioral task on spatial tuning in the visual stimulus period, for cells with weak stimulus-period spatial tuning during visual trials. All neurons for which the stimulus-period response differentials for visual trials are within the observed range of stimulus-period response differentials for auditory trials (−10.1–17.2 Hz) are included in this plot (134 cells total). Conventions are the same as in Fig. 4. No behavioral modulation of response differentials can be detected. Slope of the best-fit line, and 95% confidence intervals on the slope: 0.96 [0.79 1.16].

tuned responses to auditory stimuli in at least one of the two tasks. The results of this analysis (not shown) indicate that all trends evident in Fig. 4 persist when the data set is restricted to include only auditory cells. Thus, even among neurons with significant (and strongly task-dependent) auditory responses, visual responses are not significantly modulated by behavioral task. Behavioral modulation is therefore a specific characteristic of auditory responses in area LIP, rather than a general feature of both auditory and visual responses for a distinct subpopulation of LIP neurons.

Behavioral modulation: delay and saccade/hold periods

Many neurons recorded in area LIP responded during the delay and saccade periods of both auditory and visual memory-saccade trials, but not during the delay and hold periods of fixation trials. Figure 6 shows an example of stimulus-period, delay-period, and saccade-period activity recorded from a single LIP neuron during auditory and visual trials of the memory-saccade task. As in Fig. 2, neural activity is aligned on stimulus onset. The response of this neuron is spatially tuned in the delay and saccade periods as well as in the stimulus period, for both auditory and visual memory-saccade trials (Mann-Whitney test, $P < 0.005$ for all 3 periods and both trial types). In the fixation task (not shown), only the response in the visual stimulus period is significantly tuned.

Across the population, spatially tuned responses tend to be stronger during the delay and saccade periods of the memory-saccade task than during the delay and hold periods of the fixation task, as illustrated in Fig. 7. This figure is identical to Fig. 4, except that response differentials for the delay and saccade/hold periods are displayed instead of response differentials for the stimulus and prestimulus periods. Response differentials for the delay period and the saccade/hold period are significantly modulated by task in both auditory and visual trials (binomial test, $P < 0.01$ in all plots; all slopes significantly less than 1). Note that behavioral modulation in the

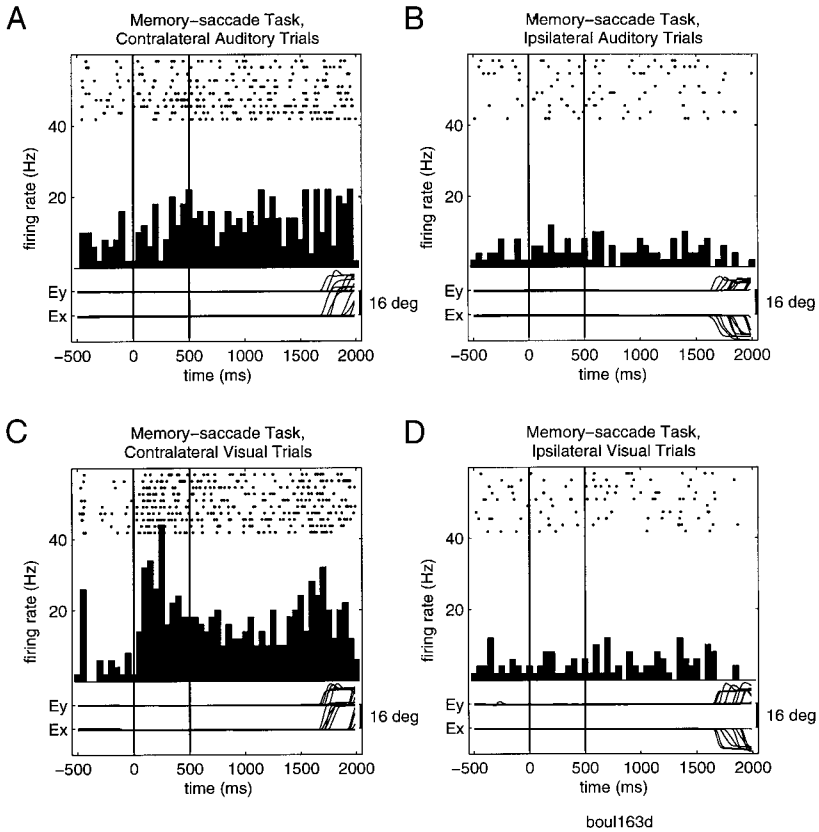

FIG. 6. Activity of an LIP neuron during auditory and visual memory-saccade trials. Each plot shows neural activity from 500 ms before stimulus onset to 2,000 ms after stimulus onset. The 2 vertical lines in each plot bracket the stimulus presentation interval; the variable delay interval extends for 800–1,300 ms after stimulus offset. Large deviations in eye position traces are saccades made during the saccade period. *A* and *B*: neural activity during the memory-saccade task for trials in which an auditory stimulus was presented at the contralateral (*A*) or ipsilateral (*B*) stimulus location. Response differentials are significant in all 3 periods (stimulus period 6.4 Hz, $P < 0.005$; delay period 8.9 Hz, $P < 0.001$; saccade period 6.4 Hz, $P < 0.001$). *C* and *D*: neural activity during contralateral (*C*) or ipsilateral (*D*) visual memory-saccade trials. Response differentials are significant in all 3 periods (stimulus period, 19.2 Hz, $P < 0.001$; delay period, 10.2 Hz, $P < 0.001$; saccade period, 9.9 Hz, $P < 0.001$). In the fixation task (not shown), spatial tuning is significant only during the visual stimulus period (response differentials for stimulus, delay, and hold periods of fixation task: auditory 0.6, 0.6, and −0.4 Hz; visual 18.6, 2.0, and 0.9 Hz).

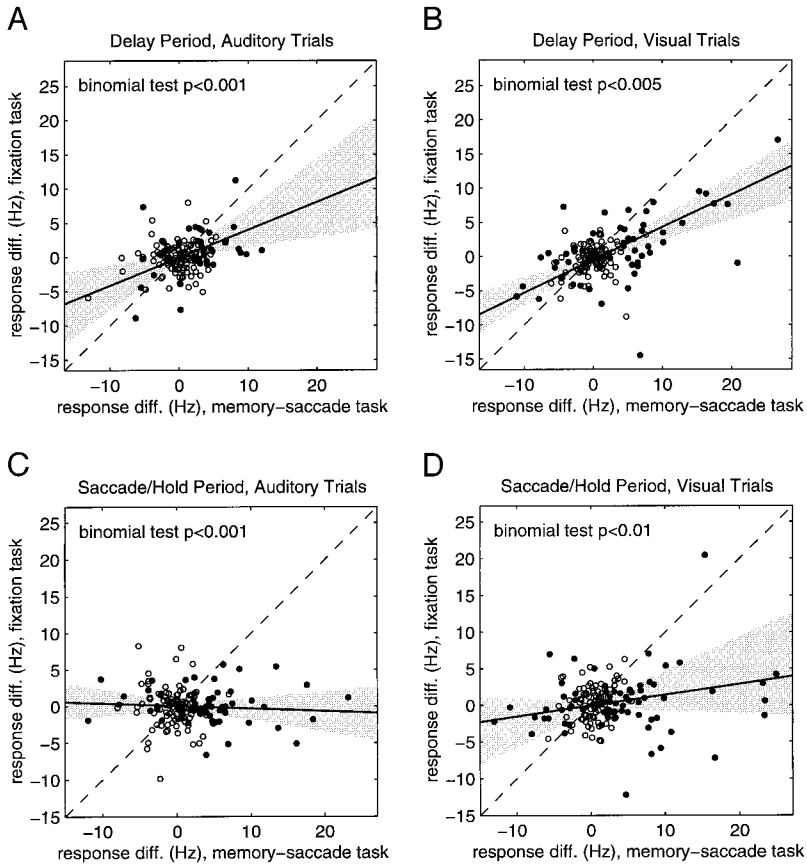

FIG. 7. Effects of behavioral task on spatial tuning in the delay and saccade/hold periods, for all 160 neurons in the database. Conventions are the same as in Fig. 4. *A* and *B*: response differentials in the delay period are significantly modulated by behavioral task during both auditory (*A*) and visual (*B*) trials. *C* and *D*: behavioral modulation is also significant in the saccade/hold period, for both auditory (*C*) and visual (*D*) trials. Slopes of the best-fit lines, and 95% confidence intervals on the slopes: *A*, 0.41 [0.15 0.73]; *B*, 0.48 [0.31 0.61]; *C*, −0.04 [−0.19 0.09]; *D*, 0.15 [−0.04 0.48].

delay period (Fig. 7, *A* and *B*) resembles behavioral modulation in the stimulus period of auditory trials (Fig. 4*A*). The slopes of the best-fit lines in Fig. 7, *A* and *B* (and in Fig. 4*A*) are significantly less than one but greater than zero, whereas the slopes in Fig. 7, *C* and *D*, are not significantly greater than zero.

As the slopes in Fig. 7, *A* and *B*, suggest, response differentials in the memory-saccade task and the fixation task are significantly correlated in the delay period for both auditory trials (Spearman rank correlation coefficient $r_s = 0.23$, $P < 0.005$) and visual trials ($r_s = 0.40$, $P < 0.001$). Note that in the delay period, the only difference between the two tasks is the presumed behavioral state of the animal. In the memory-saccade task, the monkey is assumed to be remembering the location of the stimulus and planning an eye movement, whereas in the fixation task, the monkey is assumed to be concentrating on fixating. If these assumptions were incorrect (if, for instance, the monkey were planning to make a saccade to the remembered stimulus location after the reward in the fixation task), then response differentials in the delay period of the fixation task might be correlated with response differentials in the delay period of the memory-saccade task. In other words, one possible explanation for the correlation between memory-saccade and fixation response differentials during the delay period is that the monkeys interpreted the fixation task as an unusually complicated, very-long-delay version of the memory-saccade task.

One piece of evidence against this hypothesis is that correlation between the two tasks is much weaker in the saccade/hold period ($r_s = -0.08$, n.s. for auditory trials; $r_s = 0.17$, $P < 0.05$ for visual trials). If the monkeys were making saccades after the reward in the fixation task, correlation between the two tasks should have persisted in the saccade/hold period, because neural activity associated with saccade preparation should have appeared in both the saccade period of the memory-saccade task and the hold period of the fixation task. The relatively weak response correlation in the saccade/hold period might therefore be interpreted as an indication that the monkeys were not planning memory saccades after the reward in the fixation task. However, because the behavioral requirements of the two tasks are different in the saccade/hold period, it is conceivable that response correlation might decrease in that period regardless of the monkey's behavior after the reward.

The possibility still remains, then, that delay-period correlations might arise because the monkeys made memory saccades after the reward in the fixation task. To address this possibility directly, eye position was recorded after the reward in every fixation trial, and saccadic eye movements were identified using eye velocity criteria (optimized by visual inspection of eye traces). In the majority of fixation trials, the monkey did indeed make a single saccade within 500 ms after the reward. However, these postreward eye movements did not appear to be directed toward the stimulus locations. Postreward saccades, when they occurred, were similar for contralateral and ipsilateral trials, and seemed to be highly stereotyped movements toward a default eye position slightly off the fixation point. To quantify these observations, eye positions at the end of the first postreward saccade (or at the end of the postreward recording period, for trials in which no saccade

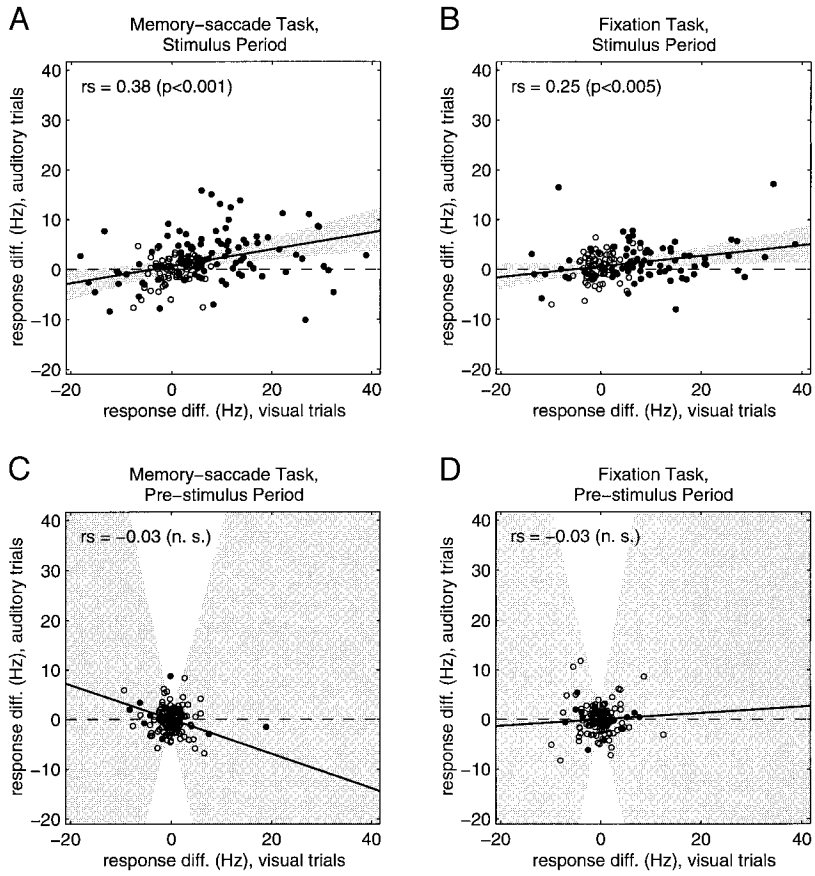

FIG. 8. Effects of trial modality on spatial tuning, stimulus, and prestimulus periods. Each panel shows the response differential during auditory trials plotted against the response differential during visual trials, for all 160 neurons in the database. ●, cells with a significant response differential in either auditory or visual trials; ○, cells for which neither response differential is significant. The Spearman rank correlation coefficient r_s is indicated on each plot, along with the significance level for rejection of the null hypothesis (no correlation). Solid line in each plot is the 2-dimensional least-mean-squares linear fit to the data; dotted line represents zero slope. Ninety-five percent confidence intervals on the slope, calculated using a bootstrap technique, are indicated in gray. *A* and *B*: during the stimulus period, auditory and visual response differentials are significantly correlated in both the memory-saccade task (*A*) and the fixation task (*B*). *C* and *D*: no significant correlation between auditory and visual trials can be detected in the prestimulus period in either task. Slopes of the best-fit lines, and 95% confidence intervals on the slopes: *A*, 0.17 [0.07 0.28]; *B*, 0.11 [0.02 0.20]; *C*, −0.35 [−4.88 3.89]; *D*, 0.06 [−4.14 5.65].

could be detected) were analyzed separately for every neural recording in the database. Recordings for which horizontal eye position distributions after the reward differed significantly between contralateral and ipsilateral fixation trials (Kolmogorov-Smirnov test, significance level 0.05) were judged to be contaminated by possible goal-directed movements. By this test, possible goal-directed eye movements occurred after auditory fixation trials in 6 of 160 recordings, and after visual fixation trials in 31 of 160 recordings. When these potentially problematic recordings are excluded from further consideration, memory-saccade and fixation response differentials are still significantly correlated in the delay period ($r_s = 0.22$, $P < 0.01$ for auditory trials in reduced dataset; $r_s = 0.41$, $P < 0.001$ for visual trials in reduced dataset). Therefore the observed correlation between delay activity in the memory-saccade task and delay activity in the fixation task cannot be attributed to overt postreward eye movements in the fixation task. It is possible, however, that goal-directed eye movements might be planned in the delay period of the fixation task but then canceled in the hold period.

Correlation between auditory and visual trials: stimulus period

Like the cell shown in Fig. 6, many neurons recorded in area LIP responded to both auditory and visual stimuli in at least one of the two tasks. The association between auditory and visual responses across the population is illustrated in Fig. 8. Response differentials in the stimulus period of auditory trials are significantly correlated with response differentials in the stimulus period of visual trials (Fig. 8, *A* and *B*) for both the memory-saccade task ($r_s = 0.38$, $P < 0.001$) and the fixation task ($r_s = 0.25$, $P < 0.005$). The correlation coefficients for both tasks are not only significantly different from zero but also positive, indicating that the direction of spatial tuning tends to be similar for auditory and visual responses recorded from the same neuron. The low slopes of the best-fit lines in Fig. 8, *A* and *B*, confirm earlier observations that responses to auditory stimuli are generally weaker than responses to visual stimuli. For comparison, response differentials in the prestimulus period are shown in Fig. 8, *C* and *D;* no correlation between auditory and visual trials is evident in the prestimulus period for either task ($r_s = -0.03$, n.s. for both tasks).

Further evidence that auditory responses tend to be associated with visual responses emerges from the anatomic distribution of neurons with auditory or visual responses. Figure 9 shows the distribution across electrode penetration sites of neurons with significant spatially tuned auditory or visual responses in the stimulus period of the memory-saccade task. [A similar figure in the accompanying paper (Grunewald et al. 1999) shows the distribution of neurons with significant spatially tuned auditory or visual responses in the stimulus period of the fixation task.] In both monkeys, all penetration sites that produced cells with spatially tuned auditory responses also produced cells with spatially tuned visual responses. Moreover, neurons with auditory responses and neurons with visual responses are distributed across all the penetration sites, with no evident clustering. This overlap of auditory and visual data across penetration sites suggests that neurons with spatially

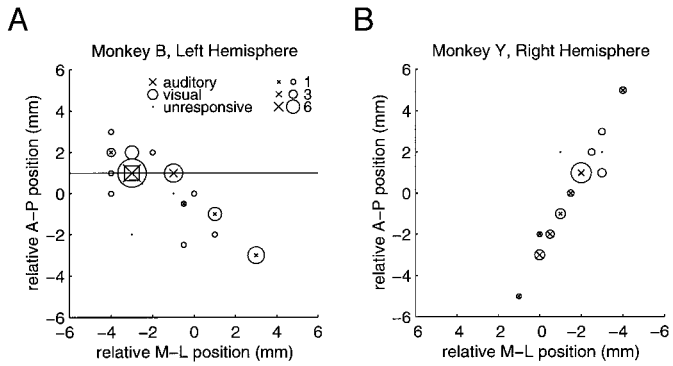

FIG. 9. Distribution across electrode penetration sites of neurons with significant spatially tuned auditory or visual responses in the stimulus period of the memory-saccade task. Each plot shows the positions of all electrode penetration sites, in mm anterior-posterior (A-P) and mm medial-lateral (M-L) relative to the center of the recording chamber. Penetration sites at which cells with spatially tuned auditory stimulus-period responses were found are labeled with a cross (×); sites at which cells with spatially tuned visual stimulus-period responses were found are labeled with an open circle (○); and sites at which no cells with tuned stimulus-period responses were found are labeled with a dot (·). The sizes of cross and circle symbols at each site are scaled to reflect the number of neurons with the corresponding type of response. *A*: electrode penetration sites for *monkey B*, whose recording chamber was mounted over the left hemisphere. The square shows the site of one of the electrolytic lesions made in this animal, and the line indicates the approximate angle of the histological section shown in the accompanying paper (Grunewald et al. 1999). *B*: electrode penetration sites for *monkey Y*, whose recording chamber was mounted over the right hemisphere. In both monkeys, cells with auditory or visual responses are intermingled across penetration sites.

tuned responses to auditory stimuli are well integrated with visually responsive neurons across area LIP.

Correlation between auditory and visual trials: delay and saccade/hold periods

Correlation between auditory and visual trials occurs in the delay and saccade periods of the memory-saccade task, as well as in the stimulus period. Across the population of recorded cells, response differentials for auditory and visual trials are significantly correlated in the delay ($r_s = 0.57$, $P < 0.001$) and the saccade ($r_s = 0.66$, $P < 0.001$) periods of the memory-saccade task (Fig. 10, *A* and *C*). Like the stimulus-period correlation coefficients, these delay- and saccade-period correlation coefficients are not only significantly different from zero but also positive, indicating consistent spatial tuning for delay/saccade activity recorded from the same neuron during auditory and visual memory-saccade trials. No significant correlation between auditory and visual trials is evident in response differentials for either the delay period or the hold period of the fixation task (Fig. 10, *B* and *D*).

Correlation between stimulus, delay, and saccade periods

Studies of visual responses in area LIP have noted that many visually responsive neurons are active in the delay or saccade periods of a memory-saccade task (Barash et al. 1991a). Are cells with auditory responses even more likely to exhibit delay

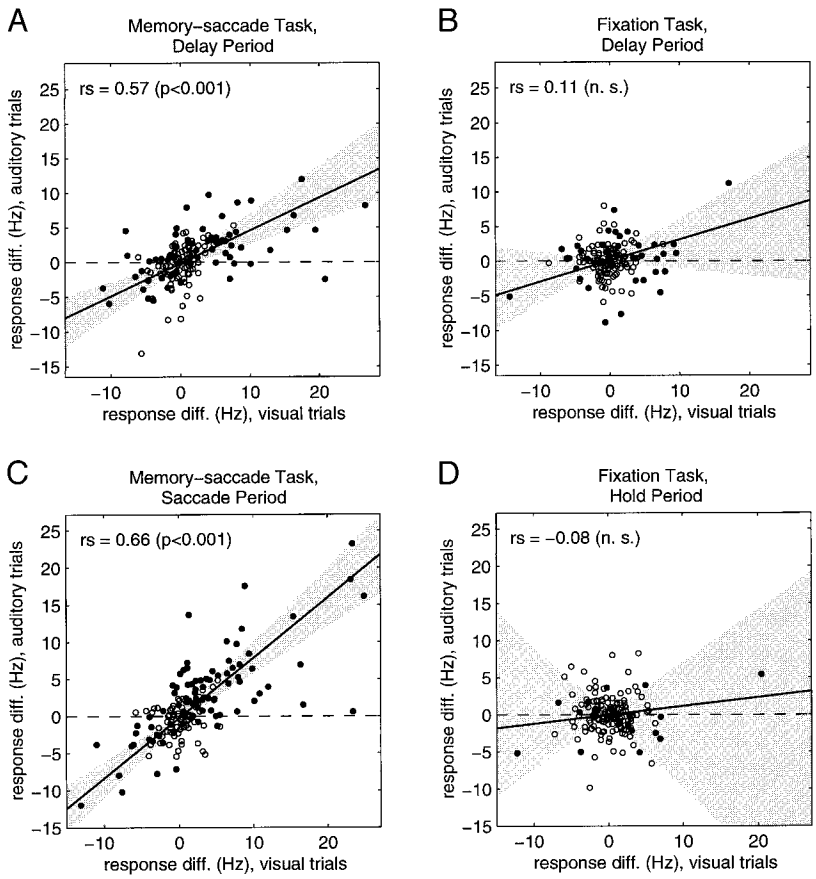

FIG. 10. Effects of trial modality on spatial tuning in the delay and saccade/hold periods, for all 160 neurons in the database. Conventions are the same as in Fig. 8. *A* and *C*: response differentials during auditory and visual trials are significantly correlated in the delay (*A*) and saccade (*C*) periods of the memory-saccade task. *B* and *D*: no significant correlation between auditory and visual trials can be detected in the delay (*B*) or hold (*D*) periods of the fixation task. Slopes of the best-fit lines, and 95% confidence intervals on the slopes: *A*, 0.47 [0.32 0.70]; *B*, 0.30 [−0.11 0.59]; *C*, 0.81 [0.62 1.01]; *D*, 0.12 [−0.96 0.71].

or saccade activity than cells with visual responses? Because auditory responses tend to co-occur with visual responses, this question is best addressed through comparison of two populations of neurons selected to be distinct: those with significantly tuned auditory (and possibly visual) responses in the stimulus period, and those with significantly tuned visual but not auditory responses. In the memory-saccade task, 66% (23/35) of neurons with spatially tuned auditory responses in the stimulus period also have delay-period responses, whereas 39% (25/64) of neurons with exclusively visual stimulus-period responses are active during the delay period. Thus neurons with auditory stimulus-period responses are significantly more likely than neurons with exclusively visual stimulus-period responses to exhibit delay activity (Fisher-Irwin test, $P < 0.05$). Delay-period responses were pooled across auditory and visual trials to obtain the above results; however, significant associations between auditory responses and delay activity are also found when delay-period responses are considered separately for auditory and visual trials.

Results for the saccade period are similar. Over 77% (27/35) of neurons with auditory stimulus-period responses in the memory-saccade task respond during the saccade period, whereas 52% (33/64) of exclusively visual cells respond during the saccade period. Neurons with auditory responses in the stimulus period are therefore significantly more likely to show saccade activity than neurons with exclusively visual stimulus-period responses (Fisher-Irwin test, $P < 0.05$). Again, this trend is evident not only when saccade-period responses are pooled across auditory and visual trials, but also when auditory and visual trials are considered separately.

These results indicate that auditory responses in the stimulus period of the memory-saccade task are more closely linked to delay and saccade activity than are exclusively visual responses. Could auditory responses be used to identify a subpopulation of visually responsive neurons in area LIP that are likely to be active in later phases of the memory-saccade task? To find out, two populations of visually responsive neurons can be compared (Fig. 11): bimodal cells, defined to be neurons with spatially tuned stimulus-period responses during both visual and auditory memory-saccade trials; and unimodal (exclusively visual) cells, defined to be neurons with spatially tuned stimulus-period responses during visual but not auditory memory-saccade trials. Figure 11, *A–D,* shows data taken from visual trials of the memory-saccade task; Fig. 11, *A* and *C,* displays data from bimodal cells, whereas Fig. 11, *B* and *D,* displays data from unimodal visual cells. The division of visually responsive neurons between the left and right halves of the figure is therefore determined entirely by the presence or absence of auditory responses. As shown in the figure, the correlation between stimulus-period response differentials and delay-period response differentials during visual trials is much stronger for neurons with both auditory and visual stimulus-period responses than for neurons with exclusively visual stimulus-period responses (bimodal cells: $r_s = 0.70$, $P < 0.001$; unimodal visual cells: $r_s = 0.20$, n.s.). The difference between the two correlation coefficients is significant (Fisher *z*-transformation test, $P < 0.01$), and the slope of the best-fit line in Fig. 11*A* is significantly greater than the slope of the best-fit line in Fig. 11*B.* The distinction between bimodal and unimodal visual cells is weaker in the saccade period (Fig. 11, *C* and *D*); although the correlation coefficient is slightly larger and

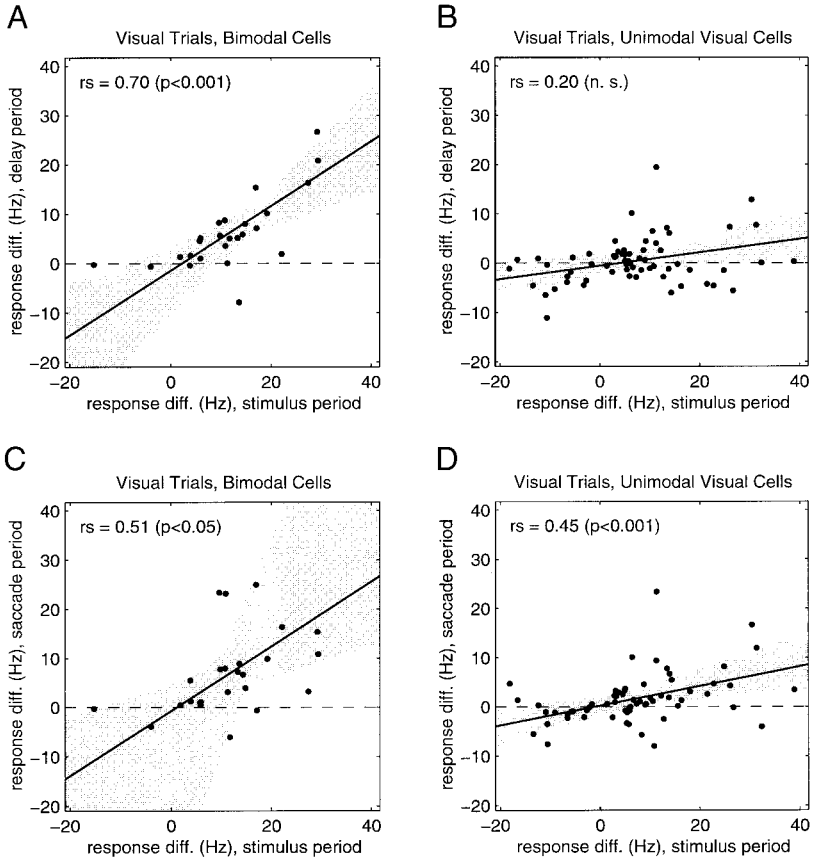

FIG. 11. Relationship between spatial tuning in the delay or saccade periods and spatial tuning in the stimulus period, for visual memory-saccade trials only. Bimodal cells are neurons with significant spatially tuned responses in the stimulus period during both auditory and visual memory-saccade trials (25 cells total). Unimodal visual cells are neurons with significant spatially tuned responses in the stimulus period during visual memory-saccade trials only (64 cells total). Other conventions are the same as in Fig. 8. In each plot, the gray area representing the 95% confidence intervals on the slope of the best-fit line has a bow-tie shape, because the bootstrapped fit lines from which the confidence intervals were determined varied in intercept. Intercept variation is also present, but not so noticeable, in previous figures. *A* and *B*: response differentials in the delay period of visual memory-saccade trials are significantly correlated with response differentials in the stimulus period for bimodal cells (*A*), but not for unimodal visual cells (*B*). *C* and *D*: correlation between response differentials in the saccade and stimulus periods of visual memory-saccade trials is significant for both bimodal (*C*) and unimodal visual (*D*) cells. Slopes of the best-fit lines, and 95% confidence intervals on the slopes: *A,* 0.65 [0.33 1.08]; *B,* 0.14 [0.02 0.26]; *C,* 0.66 [0.31 2.78]; *D,* 0.20 [0.08 0.34].

the slope of the best-fit line higher for bimodal cells than for unimodal visual cells, these differences are not significant.

The association between auditory responses and activity in later periods of the memory-saccade task suggests that auditory responses themselves might be saccade related. Analysis of error trials (memory-saccade trials in which the monkeys made saccades to the incorrect location) could, in principle, be used to determine whether auditory responses are in fact more dependent on the upcoming saccade trajectory than on the auditory stimulus location. Unfortunately, the statistical power of error trial analysis was very low for this data set, because there were few error trials. Comparison of stimulus-period response differentials for error trials with stimulus-period response differentials for correct trials revealed neither significant anti-correlation nor significant correlation, and was therefore inconclusive. Analyses of possible relationships between auditory responses and saccade parameters in correct trials were also inconclusive.

Control for response measure

Raw response differentials reflect the magnitude of spatial tuning, a quantity that is only indirectly related to the significance of spatial tuning. Analyses of response-differential distributions (Figs. 4, 5, 7, 8, 10, and 11) might therefore overemphasize data from high-firing but poorly tuned cells. To control for possible artifacts associated with the use of raw response differentials, all analyses of response-differential distributions were repeated using three different normalized response measures: *1*) the response differential normalized by the mean prestimulus-period firing rate, a measure of spatial tuning relative to background activity; *2*) the response differential normalized by the response sum (mean contralateral response plus mean ipsilateral response), a measure of spatial tuning relative to overall response; and *3*) the response differential normalized by its estimated standard error, a direct measure of the significance of spatial tuning. Results obtained using all three normalized measures are consistent with those shown for raw response differentials.

Control for block order

For each neural recording in this experiment, blocks of memory-saccade and fixation trial data were always collected in the same order: first a block of memory-saccade trials, then a block of fixation trials, and so on in alternation, for as long as the isolation could be maintained. On average, then, blocks of fixation trials were collected later in each recording than blocks of memory-saccade trials. Stronger spatial tuning in the memory-saccade task than in the fixation task could, in principle, arise from systematic changes (such as a decrease in overall firing rate) over the course of each recording. One control for such effects has already been shown; response differentials in the prestimulus period do not appear to be modulated by task (Fig. 4, *C* and *D*). As an additional control, response differentials in the first block of fixation trials were compared with response differentials in the second block of memory-saccade trials (for the 81 recordings with at least 1 block of fixation trials and 2 blocks of memory-saccade trials). Thus for this analysis, data were selected such that fixation blocks were collected earlier in each recording than memory-saccade blocks. All trends in Figs. 4, 5, and 7 were also evident in this control analysis, confirming that observed behavioral modulation effects are not an artifact of block order.

DISCUSSION

The main result of the present study is that neurons in area LIP respond more strongly to auditory stimuli when monkeys are engaged in a memory-saccade task than when they are engaged in a fixation task. Additional findings are as follows: *1*) visual responses, unlike auditory responses, are not significantly modulated by behavioral task; *2*) behavioral modulation of auditory responses resembles behavioral modulation of delay-period activity; *3*) auditory responses are associated with visual responses in both the memory-saccade task and the fixation task; and *4*) auditory responses are also associated with delay or saccade activity. Taken together, these results imply that auditory responses in area LIP are best considered supramodal (cognitive or motor) responses, rather than modality-specific sensory responses.

In combination with the results of the companion paper (Grunewald et al. 1999), which show that auditory responses appear in the fixation task only after auditory-saccade training, these findings indicate that the last of the four possibilities raised in the INTRODUCTION is correct: responses to auditory stimuli in area LIP depend both on training and on behavioral context. Therefore the resolution to the apparent discrepancy between early studies of area LIP, which found no responses to auditory stimulation (Hyvärinen 1982; Koch and Fuster 1989; Mountcastle et al. 1975), and later studies, which did find auditory responses in LIP (Mazzoni et al. 1996a; Stricanne et al. 1996), is that the monkeys had both learned an auditory-saccade task and been required to perform this task in the latter but not the former study. Further implications of the results, and interpretations in light of previous studies, are discussed below.

Behavioral modulation of auditory responses

Responses to auditory stimuli in area LIP are strongly modulated by behavior, whereas responses to visual stimuli do not appear to be dependent on task. Behavioral modulation of auditory responses is not a necessary consequence of weak spatial tuning, nor a general feature of all stimulus-period responses for cells that respond to auditory stimuli. Moreover, no behavioral modulation is observed in the prestimulus period, and behavioral modulation is not an artifact of trial block order. Behavioral modulation therefore seems to be a robust and distinctive characteristic of auditory responses in area LIP.

This study is the first to show that auditory responses in area LIP are dependent on behavioral task. However, behavioral modulation of auditory responses has previously been observed in several regions of the brain that are directly interconnected with area LIP. Neurons in the deep layers of the superior colliculus, for example, respond to auditory stimuli in the context of a saccade task, but habituate rapidly to auditory stimuli when no saccade is required (Jay and Sparks 1984, 1987b). Neurons in the prefrontal cortex also respond to auditory stimuli more strongly in the context of goal-directed (arm and eye) movements than in the context of an auditory detection or a passive listening task (Vaadia et al. 1986). Responses

to auditory stimuli in these areas, and responses to auditory stimuli in area LIP, may best be considered cognitive or motor responses, related primarily to the signficance of the stimulus as a potential target for movement.

No behavioral modulation of visual responses?

Across the population of neurons recorded in this study, visual responses and background (prestimulus) activity are not significantly modulated by behavioral task. This result seems to contradict recent reports that visual responses and background activity in area LIP are enhanced in a memory-saccade task relative to a fixation task (Colby et al. 1996). Even when reanalyzed using the analysis methods described in Colby et al. (1996), to compare maximal responses rather than response differentials in the two tasks, the data collected in the present experiment still show no evidence for behavioral modulation of visual responses in the stimulus period (for either monkey alone or for both together), and no evidence for modulation of responses in the prestimulus period. The apparent discrepancies between the present study and Colby et al. (1996) are therefore not likely to be due to differences in data analysis methods.

The discrepancies between the present study and that of Colby et al. (1996) might, however, arise from differences in behavioral paradigms and recording procedures. For the present experiments, two fixed stimulus locations were used, and stimulus presentations were randomized across the two locations. The monkeys therefore did not know which of the two possible stimulus locations would be relevant on any given trial until the stimulus actually appeared. In contrast, Colby et al. (1996) optimized the stimulus location for each cell and then used that one stimulus location for all experiments on the cell. Their monkeys therefore knew the location of the relevant stimulus even before it appeared on a given trial. Colby et al. (1996) did suggest that the background enhancement they observed in the memory-saccade task might have arisen because the monkeys were anticipating the onset of the behaviorally relevant stimulus in the receptive field. Another possibility is that enhancement of both background activity and visual responses occurred in the memory-saccade task because the monkeys were planning the impending movement (Bracewell et al. 1996; Mazzoni et al. 1996b; Platt and Glimcher 1997; Shadlen and Newsome 1996).

Behavioral modulation of delay activity

Neurons in area LIP are more active in the delay and saccade periods of the memory-saccade task than in the delay and hold periods of the fixation task, for both auditory and visual trials. This result was expected. In the memory-saccade task, the monkey must remember the location of a previously presented stimulus, plan an eye movement, and execute a saccade. Delay activity is thought to reflect motor intention or spatial attention that would be engaged in the delay period of the memory-saccade task but not in the delay period of the fixation task. Similarly, saccade activity should occur only in the saccade period of the memory-saccade task, not in the hold period of the fixation task.

A more unexpected finding is that behavioral modulation in the delay period resembles behavioral modulation in the auditory stimulus period. Like auditory responses, delay-period responses are weaker, on average, during fixation trials than during memory-saccade trials, but some activity does persist in the fixation task. Indeed, response differentials in the delay period of fixation trials are significantly correlated with response differentials in the delay period of memory-saccade trials. This correlation might be considered evidence that the animals did not fully realize that they were supposed to be performing a fixation task (rather than a very-long-delay version of the memory-saccade task). Certainly, delay-period activity is usually associated with movement planning or peripherally directed attention, neither of which was required in the fixation task. For three reasons, however, it seems very unlikely that the animals were misinterpreting the fixation task. First of all, the behavioral paradigm for fixation trials ensured that eye movements toward the stimulus locations within 1,500–2,500 ms after stimulus offset would cause the trial to be aborted. Second, the use of trial blocking and task cues (steady fixation light onset in memory-saccade trials, flashing onset in fixation trials) made the presentation of fixation trials entirely predictable. Third, the correlation does not disappear when the data set is restricted to recordings that are unlikely to be contaminated by very late, goal-directed eye movements in the fixation task.

Rather than aberrant behavioral strategies, the observed correlation in delay-period response differentials may reflect covert orienting responses or attentional effects. Auditory and visual stimuli may evoke default movement plans or sustained attentional orienting that activate area LIP during the delay period of the fixation task, even though the fixation task does not require either an eye movement or a redirection of attention. In support of this view, previous studies have demonstrated that movement plans are represented in LIP even when the movement is never executed (Bracewell et al. 1996; Snyder et al. 1997, 1998). The apparent similarity between behavioral modulation of delay activity and behavioral modulation of auditory responses therefore raises the possibility that both delay activity and auditory responses reflect default movement plans.

Association between auditory and visual responses

Neurons with auditory stimulus-period responses tend to have visual stimulus-period responses with similar spatial tuning, in both the memory-saccade task and the fixation task. Moreover, neurons that respond during the delay or saccade periods of auditory memory-saccade trials are likely to respond similarly during the corresponding periods of visual memory-saccade trials. No such correlation between auditory and visual trials can be detected in the delay or hold periods of the fixation task, or in the prestimulus period of either task. Thus correlations between auditory and visual trials occur specifically during stimulus presentations in both tasks, and during the later phases of the memory-saccade task.

These findings are consistent with the results of previous studies of auditory and visual responses, both in area LIP and in regions of the brain that are anatomically connected to area LIP. In an earlier investigation of LIP activity during auditory and visual memory-saccade trials, Mazzoni et al. (1996a) concluded that neurons active during the stimulus, delay, or saccade periods of an auditory memory-saccade task tended to be

active during the same periods of a visual memory-saccade task. The present study confirms those results and further demonstrates that an association between auditory and visual trials also exists during the stimulus period, but not later periods, of a fixation task. Similar response correlations between auditory and visual trials, either during sensory stimulation or during later phases of a movement task, have also been noted in the superior colliculus (Jay and Sparks 1984, 1987a; Wallace et al. 1996), frontal cortex (Vaadia et al. 1986), frontal and supplementary eye fields (Russo and Bruce 1994; Schall 1991b), and supplementary motor areas (Schall 1991a).

The observed correlations between auditory and visual trials during the delay and saccade periods of the memory-saccade task could be viewed as confirmation that activity during these periods is related to target selection or movement planning. Movement cues of different sensory modalities evoke similar delay and saccade activity in LIP; therefore this activity probably reflects supramodal processes, such as motor intention or spatial attention. By extension, the association between auditory and visual responses in the stimulus period implies that some component of stimulus-evoked activity in area LIP also reflects movement planning or target selection. The results therefore lend support to the idea that responses to auditory stimuli in area LIP are supramodal intentional or attentional responses, rather than modality-specific sensory responses.

Association between auditory and delay/saccade activity

Neurons with auditory stimulus-period responses are much more likely to display delay or saccade activity than neurons with exclusively visual stimulus-period responses. Moreover, in the visual memory-saccade task, correlation between stimulus-period and delay-period activity is higher for neurons with both auditory and visual stimulus-period responses than for neurons with exclusively visual stimulus-period responses. These findings suggest that neurons in area LIP that respond to auditory stimuli are more directly involved in eye-movement planning than neurons that respond to visual stimuli alone. Given the physiological similarities between area LIP, the frontal eye fields, and the deep layers of the superior colliculus, a similar association between auditory and delay- or saccade-related activity may be evident in the frontal eye fields and the superior colliculus. Previous studies of these areas have not provided data appropriate for direct comparison with the present results.

Experimental considerations

The results of the present study indicate that auditory responses in area LIP are dependent on behavioral task, associated with visual responses, and predictive of delay or saccade activity. It should be noted, however, that these findings may be dependent on the choice of experimental conditions. Four possible caveats seem especially worthy of consideration.

First, the auditory stimuli used in the present study were bursts of high-frequency band-limited white noise (5–10 kHz), which probably have little ethological significance to monkeys. Sounds with different spectral characteristics (e.g., macaque vocalizations) might conceivably elicit auditory responses in area LIP that are less dependent on behavioral task than the responses observed in the present study.

Second, in these experiments, auditory stimuli were presented only at locations within the visual field, at relatively small eccentricities (16° in azimuth, 8° in elevation; ~18° in eccentricity). Because primates may use auditory spatial cues primarily for localizing targets outside of the visual field, it is possible that auditory stimuli presented at large eccentricities might evoke auditory responses in area LIP that are not associated with visual responses. Moreover, if neurons in area LIP have auditory receptive fields that are more peripheral than their visual receptive fields, then the two fixed stimulus locations used in the present experiment might occasionally have been optimal for a neuron's visual receptive field, but might never have been optimal for any neuron's auditory receptive field. Apparent behavioral modulation of responses to auditory stimuli might turn out to be behavioral modulation of responses to suboptimal stimuli. This scenario seems unlikely, because weakly tuned visual responses (which presumably represent responses to suboptimal visual stimuli) do not appear to be modulated by task (Fig. 5); however, the possibility cannot be ruled out on the basis of the present data.

Third, the position of the pinnae was not controlled in these experiments. Therefore, the apparent link between auditory responses and eye movements might actually reflect an association between auditory responses and pinna movement. Moreover, if the monkeys moved their pinnae differently during the stimulus periods of memory-saccade and fixation trials, auditory stimuli might have been filtered differently by the ears in the two tasks, producing apparent behavioral modulation of auditory responses. Although these possibilities cannot be excluded, they seem very unlikely. Previous studies have shown that the incidence of auditory responses in area LIP, and the tuning of auditory responses in superior colliculus, are not significantly altered by pinna restraint in awake monkeys (Jay and Sparks 1987b; Stricanne et al. 1996). Furthermore, although pinna movements have not been studied intensively in monkeys, a recent behavioral study in cats suggests that pinna movements could not account for the observed behavioral modulation of auditory responses. Cats make auditory-evoked pinna movements, which do not appear to be dependent on behavioral task, and orienting pinna movements, which occur in conjunction with eye movements (Populin and Yin 1998). If we assume that these results generalize to monkeys, pinna movements in response to auditory stimulation should have been the same for the two behavioral tasks, and pinna movements in conjunction with eye movements should not have occurred until long after the auditory stimulus period.

Finally, the monkeys used in the present study performed all the behavioral tasks with their heads immobilized. Under more natural conditions, primates orient to auditory and visual stimuli with a combined movement of the head and eyes (Goldring et al. 1996; Whittington et al. 1981). Because auditory targets can be perceived at larger eccentricities than visual targets, and can therefore evoke larger orienting movements, responses to auditory stimuli may be strongly associated with free head movement. Responses to auditory stimuli in area LIP might therefore be most robust in the context of head movements, rather than eye movements.

Although these potential caveats should not be overlooked, it seems likely that the present results will generalize to other experimental conditions, because the findings are consistent with previous studies of auditory responses in areas that are

anatomically interconnected with LIP. In particular, behavioral modulation of auditory responses, and associations between auditory and visual responses, have been observed in both superior colliculus and frontal cortex under a range of different experimental conditions (superior colliculus: Jay and Sparks 1987b; Wallace et al. 1996; frontal cortex: Russo and Bruce 1994; Vaadia et al. 1986). The present findings are also consistent with current interpretations of LIP function, as discussed further in the following section.

Interpretations

The present study demonstrates that responses to auditory stimuli in area LIP are dependent on behavioral task, associated with visual responses, and predictive of delay or saccade activity. These results imply that responses to auditory stimuli in area LIP are best considered supramodal responses, not modality-specific sensory responses. Several different interpretations of these findings, and of the role of area LIP in auditory-to-oculomotor processing, are possible.

For example, auditory activity in area LIP may be related to spatial attention that is not modality specific (Colby et al. 1996; Gottlieb et al. 1998). According to this interpretation, LIP responses to auditory stimuli are stronger in the memory-saccade task than in the fixation task because the animal must attend more closely to the spatial information present in the auditory cue when a localization movement is required. The fact that auditory responses in area LIP are weaker and more dependent on behavioral task than visual responses implies, in this scenario, that auditory stimuli do not capture spatial attention as effectively as visual stimuli. Indeed, the auditory stimuli used in this experiment were probably less easy to localize (and perhaps less spatially salient) than the visual stimuli, given that the monkeys required months of training to master the auditory-saccade task but only a few days to master the visual-saccade task (see Grunewald et al. 1999).

The results of the present study are also consistent with the view that activity in area LIP reflects movement intention (Bracewell et al. 1996; Mazzoni et al. 1996b; Platt and Glimcher 1997; Snyder et al. 1997, 1998). According to this interpretation, responses to auditory stimuli in area LIP are modulated by behavioral task because auditory stimuli evoke more definite movement plans in the memory-saccade task than in the fixation task; similarly, auditory responses are more task dependent than visual responses because auditory orienting is less reflexive than visual orienting (at least for the stimuli used in this study). Residual activity in the stimulus period of auditory fixation trials, discussed further in the companion paper (Grunewald et al. 1999), represents a suppressed intention to make an eye movement to an auditory target made familiar by months of saccade training. Consistent with this interpretation, the link between auditory stimulus-period responses and delay or saccade activity in the memory-saccade task implies that responses to auditory stimuli in LIP are directly related to movement intention.

A third possible interpretation of the data is that responses to auditory stimuli in area LIP reflect oculomotor significance: the significance of the stimuli as potential targets for eye movements. By this argument, the stimulus-period auditory activity in the fixation task reflects the learned significance of the auditory stimulus as a possible eye movement target (Grunewald et al. 1999). When the sound becomes an obligate target for an eye movement in the memory-saccade task, its significance increases further. However, in the memory-saccade task, the increase in the auditory stimulus-period response is linked to the presence of continued activity in the delay period, and other experiments have shown that delay-period activity generally reflects the monkey's intention to make eye movements (Snyder et al. 1997, 1998). Thus a simpler explanation for the increase in stimulus-period activity in the auditory memory-saccade task may be that movement-planning activity is added to activity reflecting the learned significance of the auditory stimulus.

Finally, a fourth possibility is that spatial attention, motor intention, and oculomotor significance are artificial psychological distinctions for area LIP, which performs sensory-to-motor transformations for saccades. According to this view, increased activity in the stimulus period of the auditory memory-saccade task simply reflects a graded increase in the preparation for a sensory-guided eye movement.

The present study was designed to resolve discrepancies between early and more recent reports regarding auditory activity in LIP, not to distinguish between the four possible interpretations of auditory responses described above. Further research will be required to determine the degree to which behavioral modulation of auditory activity supports these different interpretations. For instance, if future experiments show that auditory stimuli evoke stronger responses in LIP when a monkey plans a saccade to an auditory target than when he plans a reach to the same target, then a significant component of auditory activity in LIP represents intention to make a saccade, independent of spatial attention. Because delay activity in LIP is linked to the eye movement plan (Snyder et al. 1997, 1998), the close association between delay activity and responses to auditory stimuli suggests that activity in the auditory stimulus period does contain a substantial intentional component. Therefore, behavioral modulation of responses to auditory stimuli in area LIP may primarily reflect selection of auditory stimuli as targets for eye movements.

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