

Change in Motor Plan, Without a Change in the Spatial Locus of Attention, Modulates Activity in Posterior Parietal Cortex

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Snyder, Lawrence H., Aaron P. Batista, and Richard A. Andersen. Change in motor plan, without a change in the spatial locus of attention, modulates activity in posterior parietal cortex. *J. Neurophysiol.* 79: 2814–2819, 1998. The lateral intraparietal area (LIP) of macaque monkey, and a parietal reach region (PRR) medial and posterior to LIP, code the intention to make visually guided eye and arm movements, respectively. We studied the effect of changing the motor plan, without changing the locus of attention, on single neurons in these two areas. A central target was fixated while one or two sequential flashes occurred in the periphery. The first appeared either within the response field of the neuron being recorded or else on the opposite side of the fixation point. Animals planned a saccade (red flash) or reach (green flash) to the flash location. In some trials, a second flash 750 ms later could change the motor plan but never shifted attention: second flashes always occurred at the same location as the preceding first flash. Responses in LIP were larger when a saccade was instructed ($n = 20$ cells), whereas responses in PRR were larger when a reach was instructed ($n = 17$). This motor preference was observed for both first flashes and second flashes. In addition, the response to a second flash depended on whether it affirmed or countermanded the first flash; second flash responses were diminished only in the former case. Control experiments indicated that this differential effect was not due to stimulus novelty. These findings support a role for posterior parietal cortex in coding specific motor intention and are consistent with a possible role in the nonspatial shifting of motor intention.

INTRODUCTION

Neural responses in the lateral intraparietal area (LIP) and an adjacent parietal reach region (PRR) of macaque monkey are related specifically to rapid goal-directed movements of the eyes and arms, respectively (Bracewell et al. 1996; Mazzone et al. 1996; Snyder et al. 1997). Previous studies suggest that portions of the parietal cortex may encode the spatial locus of visual attention or play a role in shifting visual attention (Bowman et al. 1993; Bushnell et al. 1981; Lynch et al. 1977; Robinson et al. 1978, 1995; Steinmetz et al. 1994; Steinmetz and Constantinidis 1995; Yin and Mountcastle 1977). In the current study, we tested whether a shift in motor intention, exclusive of a shift in spatial attention, might also modulate activity in LIP and PRR.

METHODS

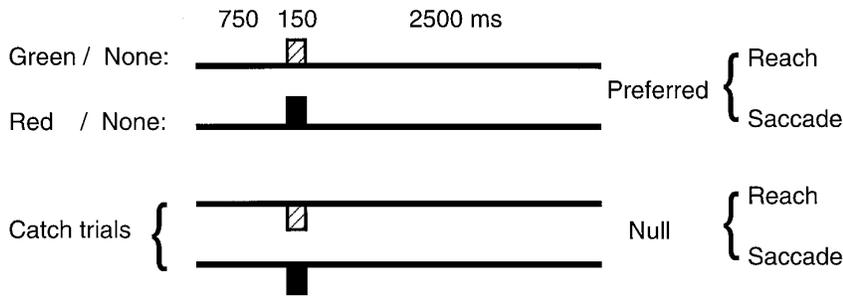
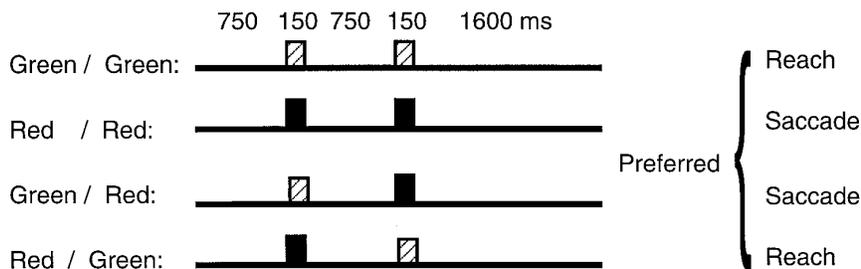
Equipment, training, and surgery have been described previously (Snyder et al. 1997). Briefly, eye movements (scleral search coil technique, 500-Hz sampling rate), button press and release times (2-ms resolution), and single unit activity (0.4-ms resolution) were

recorded for off-line analysis. A square array of eight 3.2-cm buttons surrounding a central fixation button, each of which could be lit by a red or green LED, was located 28 cm from the eyes, subtending $30 \times 30^\circ$ of visual angle. Extracellular potentials were recorded using tungsten electrodes inserted through a recording cylinder centered at 5 mm posterior and 12 mm lateral (Horsley-Clarke coordinates). Single cells were isolated while animals performed delayed saccades and reaches to one of the eight peripheral red or green LEDs. Data were collected from cells that had excitatory responses before movement to at least one target.

The effect of changes in motor intention was studied in two adult male rhesus monkeys. Trials began with 750 ms of central light fixation in an otherwise dark room (Fig. 1). A peripheral flash on opposite sides of the fixation point and either inside or outside the receptive field instructed a saccade (red) or a reach (green). On half of trials, a second flash occurred at the same location as the first, either affirming or countermanding the type of movement to be made. (Never, during training or data collection, did an animal experience a trial with sequential flashes in 2 different locations.) Thus the first flash oriented the animal's attention in space and instructed the direction and modality of an upcoming movement. The second flash always occurred at an attended location and so never shifted attention but sometimes instructed a change in movement type. Finally, the fixation light was extinguished, signaling the animal to execute the planned movement (see Fig. 1 for timing). The delay periods of single flash trials and double flash trials were 2,500 and 1,600 ms, respectively.

Eight to 12 repetitions of each trial type were performed. Trials with premature or incorrect movements were aborted and the data discarded. On randomly interleaved trials, movements opposite to the neuron's response field were instructed so that the location of the first flash, unlike that of the second, could not be predicted. Data from these catch trials are not presented. More than 90% of trials were completed successfully. In each recording session, either the ipsilateral arm (PRR recording: 13 cells; LIP: 6 cells) or contralateral arm (4 PRR cells, 14 LIP cells) was used, and the other was restrained lightly. Although this study was not designed to address this issue and quantitative data were not obtained, no systematic effect of laterality on the proportion of responsive cells was observed.

Statistical significance was calculated using a paired Student's *t*-test (population data, $P \leq 0.01$) or unpaired *t*-test (single cell data, $P < 0.05$). In LIP, data were obtained 100–450 ms after flash onset. In PRR, peak second flash responses were delayed ≤ 150 ms compared with first flash responses, and sustained activity from the first flash often continued up until and slightly beyond the time of the second flash (Figs. 2A and 3A, *middle*). To avoid contamination from this sustained first flash response and to compensate for the slowed response to the second flash, PRR activity was measured 350–550 ms after second flash onsets but 200–400 ms after first flashes. These intervals were chosen to begin at the

Single flash trials:Double flash trials:

approximate peak transient PRR response time. Because data from LIP and PRR were never directly compared, there was no compelling reason to use corresponding epochs in the two areas.

RESULTS

Data are reported for 20 LIP and 17 PRR neurons with excitatory responses to intended movements collected from two monkeys. This includes all cells with directional cue or delay period responses in a memory saccade task, recorded from nine consecutive tracks in one animal (10 cells in LIP, 15 cells in PRR) (histology shown in Fig. 3 of Snyder et al. 1997) and from eight consecutive tracks in a second animal (10 cells in LIP, 2 cells in PRR).

If parietal cortex encodes only the locus of spatial attention, then the response to a flash should not depend on the movement instructed by the flash. Furthermore, if only shifts in attention are encoded, then a flash at an attended location should elicit a diminished response, regardless of what it signifies (Steinmetz et al. 1994). Neither finding was observed. Figure 2 shows averaged responses of one PRR neuron (*A*) and one LIP neuron (*B*) to red followed by green flashes (light traces) and to green followed by red flashes (dark traces). Each pair of flashes were presented inside the response field at the same location.

In PRR, an initial flash instructing a saccade evoked a transient response (S1), whereas the instruction to reach evoked a transient plus sustained response (R1). A second flash of opposite color then was presented at the same location, instructing a change of plan from a saccade to a reach or vice versa. A flash instructing a change from a saccade to a reach evoked a much larger response (R2) than did the same flash presented first (R1). Conversely, a flash instructing a change from a reach to a saccade produced almost

FIG. 1. Time course of 8 single and double flash-delayed movement trials. Experiment was designed to force the animal to attend to the spatial location and color of both flashes. A 150-ms flash appeared 750 ms after fixation began. Red and green flashes instructed saccades and reaches, respectively. On half of the trials, a 2nd flash occurred 750 ms later at the same location as the 1st, sometimes instructing a change in the motor plan but never shifting spatial attention. Fixation light offset, 2.5 s after the 1st flash, signaled the animal to perform the most recently instructed movement. For 1 animal, double flash trials also occurred for the null direction (not shown).

no transient response and a decrease in sustained activity (S2). These reciprocal activity changes are reminiscent of those produced by Bracewell and colleagues (1996). However, those changes were produced by changing the *direction* of intended movement; the modulations shown here were produced by changing the *type* of intended movement.

A complementary pattern was observed in LIP (Fig. 2*B*). The instruction to plan a saccade evoked a larger response than the instruction to plan a reach (S1 vs. R1). This differential response occurred not just for first but also for second flashes (S2 vs. R2). Furthermore, the instruction to change the plan from a reach to a saccade (S2) resulted in a larger response than an initial saccade instruction (S1).

Figure 3 shows averaged data from PRR (*A*) and LIP (*B*). *Left panels* show first flash responses, sorted by instruction. In PRR (Fig. 3*A*), reach instructions elicited larger responses than saccade instructions: 26.2 ± 2.3 vs. 16.1 ± 1.8 (SE) spikes/s (*traces 1* vs. *2*, mean \pm SE for 17 cells; equal responses can be rejected with $P \leq 0.01$). In the majority of neurons, elevated firing continued throughout the delay period before a reach. The reverse pattern occurred in LIP (Fig. 3*B*, *left panel*): saccade instructions were preferred (30.8 ± 2.1 vs. 18.2 ± 1.5 spikes/s; $n = 20$, $P \leq 0.01$). Single cell data confirmed these patterns. Reach responses were greater in all but 1 PRR cell, and saccade responses were greater in all 20 LIP cells (Table 1, P vs. N). These data confirm the findings of Snyder et al. (1997).

In the *center and right panels* of Fig. 3, *A* and *B*, responses to second flashes are sorted by whether they instructed a preferred (*center*) or nonpreferred (*right*) movement type and by whether they affirmed (---) or countermanded (—) the previous instruction. Responses were larger when the second flash instructed a preferred move-

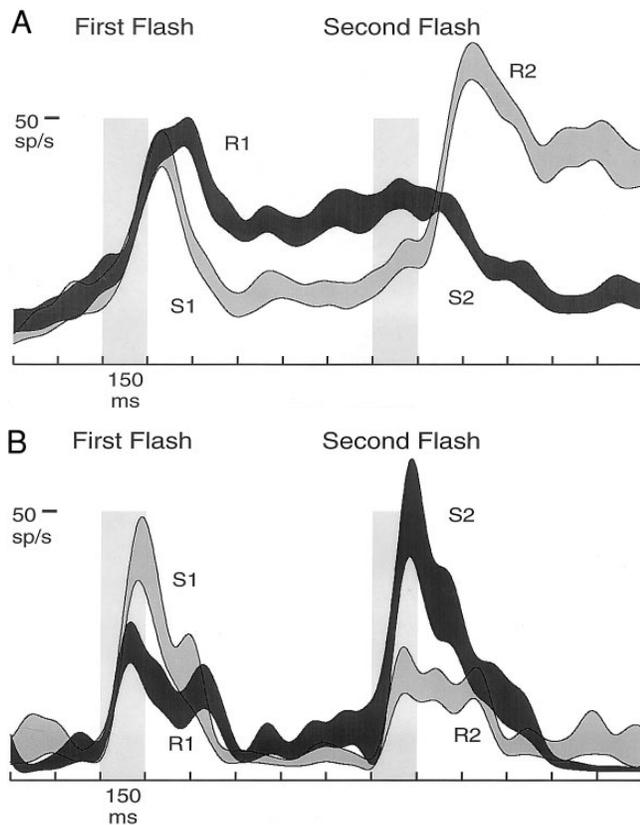


FIG. 2. *A*: intention-selective responses of a parietal reach region (PRR) neuron to changes in motor plan, from a saccade to a reach (light trace) or from a reach to a saccade (dark trace). Sustained activity resulting from an instruction to plan a reach (R1) was abolished when a second flash changed the plan to a saccade (S2). An initial instruction to plan a saccade elicited only a transient response (S1), but when the plan was changed to a reach, activity increased (R2). Instruction to plan a reach elicited a larger response when countermanding a previous plan than when presented alone (R2 transient and sustained responses are larger than R1 responses). Reverse was true for a flash instructing a saccade (S2 transient less than S1 transient). Each flash was presented at the same location inside the response field so that second flashes changed motor intention without shifting spatial attention. All data shown were obtained before movement was cued to begin. *B*: intention-selective responses from a lateral intraparietal area (LIP) neuron, complementary to the neuron of *A*. Flashes instructing saccades elicited larger responses than those instructing reaches (S1 vs. R1 and S2 vs. R2) with still larger transient responses when the instruction to saccade countermanded a previous instruction (S2 vs. S1). Each ribbon is the mean response of 8–12 trials \pm 1 SE. Shading indicates the time of one 150-ms flash. Data were smoothed before plotting (191 point digital low-pass filter, transition band 20–32 Hz), but all reported values were obtained before smoothing.

ment (*traces 3 and 4*) compared with a nonpreferred movement (*traces 5 and 6*): 23.3 ± 3.4 versus 12.9 ± 2.6 spikes/s in PRR and 31.2 ± 3.5 versus 20.8 ± 3.0 spikes/s in LIP, both significant at $P \leq 0.01$. Preferred and nonpreferred here refer to movement type, not direction; all data presented are for movements planned into the response field.

Responses in the *center and right panels* are further split according to whether the second flash countermanded (Fig. 3*A*, *traces 3 and 5*, —) or affirmed (Fig. 3*A*, *traces 4 and 6*, - - -) the previous instruction. A countermanding, preferred second flash (*3*) elicited a response comparable to or larger than the same flash presented first (*1*): 30.4 ± 3.8

versus 26.2 ± 2.3 spikes/s in PRR and 33.6 ± 3.8 versus 30.8 ± 2.1 spikes/s in LIP (both $P \geq 0.05$). This was the case despite the fact that first but not second flashes shifted the locus of attention, suggesting that a component of LIP and PRR activity reflects the setting up of specific motor plans and not the location of spatial attention.

Steinmetz and colleagues reported a very different effect in 7*a*: repeated flashes at the same location elicited reduced responses (Steinmetz et al. 1994; Steinmetz and Constantinidis 1995). In PRR and LIP, responses to a second flash were reduced if the two flashes instructed the same movement (Fig. 3, *A and B*, *trace 4 vs. 1*): 16.1 ± 3.1 versus 26.2 ± 2.3 in PRR and 28.9 ± 3.3 versus 30.8 ± 2.1 in LIP ($P \leq 0.01$ in PRR). Single cell data confirm these findings with stronger effects in PRR than in LIP. An *affirming* second flash elicited a significantly decreased response (compared with that elicited by the same flash presented first) in 16 cells and an increased response in only 2 (Table 1, P/P vs. P). In contrast, a *countermanding* second target elicited significantly decreased responses in only 3 cells but significantly increased responses in 10. Therefore the decrement seen by Steinmetz et al. in 7*a*, whereby responses to stimuli presented at an attended location were reduced, was evident in LIP and PRR only when the stimulus affirmed the existing motor plan. If the stimulus signaled a change in motor plan, the effect was reversed, and a similar or even increased response occurred. This is again consistent with the idea that a large component of LIP and PRR activity reflects specific motor intention, and not the location of spatial attention.

A strong test of the motor intention hypothesis is to compare responses to the same second flash when it either affirms (—) or countermands (- - -) the first instruction. A flash instructing a preferred movement evoked a greater response when it countermanded rather than affirmed the preceding flash (*traces 3 vs. 4*: 30.4 ± 3.8 vs. 16.1 ± 3.1 spikes/s in PRR; 33.6 ± 3.8 vs. 28.9 ± 3.3 in LIP; both $P \leq 0.01$). The small but significant effect in LIP was consistent across the two animals. This suggests that LIP and PRR activities are modulated by changes in the intended motor plan.

From these data alone, we cannot rule out an alternative explanation: a novel color elicits a greater response than a familiar color. However, responses to second flashes instructing *nonpreferred* movements do not support a role of novelty, as they did not depend on the preceding flash (*traces 5 vs. 6*: 12.3 ± 2.6 vs. 13.4 ± 2.7 spikes/s in PRR; 22.6 ± 2.8 vs. 19.0 ± 3.2 spikes/s in LIP; both $P > 0.05$). Two points are worth noting. There is a late divergence of LIP responses, although the early responses are almost identical. Second, in PRR, the peak response to a countermanding nonpreferred flash was greater than that to an affirming nonpreferred flash, but this only reflects the higher sustained activity after the first flash and preceding the second; the relative increases from the two different baselines are similar. The 350- to 550-ms measurement interval for second flashes was chosen to avoid baseline contamination.

A cell by cell analysis confirmed the population data. A second flash instructing a preferred movement evoked a significantly larger response in 14 of 37 cells when it

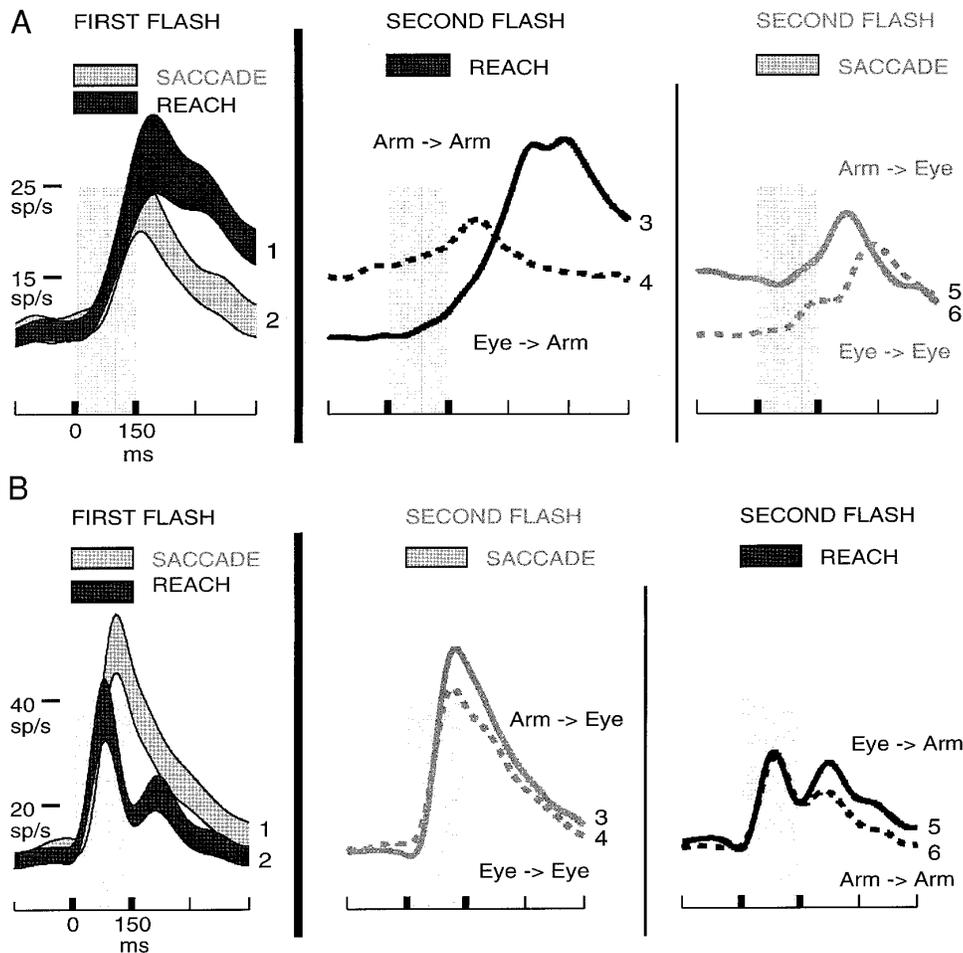


FIG. 3. Population data from PRR (A; average of 17 cells) and LIP (B; average of 20 cells). Responses to 1st (left) and 2nd (right and middle) flashes, instructing either a saccade (light) or a reach (dark) are shown. Second flashes could instruct a preferred (middle) or nonpreferred (right) movement, and this instruction could countermand (traces, 3 and 5, —) or affirm (traces, 4 and 6, - - -) the original instruction. Response to a preferred countermanding flash was larger than to a preferred affirming flash (3 vs. 4) and comparable with the response to a preferred 1st flash (1). For nonpreferred movements, countermanding and affirming flashes elicited similar comparatively small responses (5 vs. 6). Format as in Fig. 2, except that SE was calculated across cells rather than across trials (left).

countermanded rather than affirmed the first flash, with no cells showing a significant decrease (Table 1, N/P vs. P/P). If increased responses to countermanding flashes were an effect of stimulus novelty, we would expect a similar increase for countermanding nonpreferred flashes. Instead, similar numbers of cells showed increased and decreased responses, exactly as would be predicted if there were no systematic effect of novelty (Table 1, P/N vs. N/N). Therefore novelty alone cannot explain why a preferred second flash elicits a greater response when it countermands rather than affirms the first flash.

DISCUSSION

There has been considerable investigation examining the degree to which posterior parietal activity is better described as encoding sensory responses, spatial attention or motor intention (Andersen 1995; Colby et al. 1995; Gnadt and Andersen 1988; Lynch et al. 1977; Mountcastle et al. 1975; Robinson et al. 1978). Two recent findings inspired the current study. First, cells in LIP and PRR encode specifically (though not exclusively) the intention to saccade and reach, respectively (Snyder et al. 1997). Second, in 7a, responses to targets appearing at attended locations were diminished relative to responses to targets at nonattended locations, consistent with a role for 7a in shifting spatial attention (Steinmetz et al. 1994; Steinmetz and Constantinidis 1995).

In our task, a direct comparison of first and second flash responses was problematic because the animal was in a different behavioral state in each case. Before the first flash, the animal did not know which of the two possible directions to attend to, and no movement plan had been instructed. The second flash, on the other hand, either affirmed or countermanded a previously established plan and did not shift the locus of attention. Despite this difference, responses to preferred, countermanding second flashes were comparable with or greater than responses to preferred first flashes, consistent with the idea that shifts in motor intention are at least as important as shifts in attention. Another demonstration of this idea was the fact that the response to a second flash instructing a preferred movement was greater when it countermanded rather than affirmed the preceding flash (Fig. 3). Similar patterns were seen in both LIP and PRR, although the magnitude of the effects were larger in PRR.

If LIP and PRR are inhibited by nonpreferred motor plans, as suggested by the data of Snyder et al. (1997), then the larger response to a countermanding second flash could reflect a rebound from inhibition. Alternatively, the smaller response to an affirming second flash could reflect the fact that an affirming flash carries no new information and therefore is filtered out at an early stage. Additional processing that occurs only when there is already an existing motor plan could account for the increased latency of PRR responses to

TABLE 1. *Response to first or second flashes instructing movements*

Movement Instructed	PRR		LIP	
	Responses	No. of cells > vs. < No. of significantly > No. of significantly <	Responses	No. of cells > vs. < No. of significantly > No. of significantly <
Preferred vs. Null	26.2 ± 2.3**	16 vs. 1	30.8 ± 2.1**	20 vs. 0
	vs. 16.1 ± 1.8	15* 1*	vs. 18.2 ± 1.5	14* 0
-P vs. -N	23.3 ± 3.4**	15 vs. 2	31.2 ± 3.5**	20 vs. 0
	vs. 12.9 ± 2.6	11* 1*	vs. 20.8 ± 3.0	9* 0
N/P vs. P/-	30.4 ± 3.8	12 vs. 5	33.6 ± 3.8	13 vs. 7
	vs. 26.2 ± 2.3	6* 0	vs. 30.8 ± 2.1	4* 1*
P/P vs. P/-	16.1 ± 3.1**	2 vs. 15	28.9 ± 3.3	10 vs. 10
	vs. 26.1 ± 2.3	1* 13*	vs. 30.8 ± 2.1	1* 4*
N/P vs. P/P	30.4 ± 3.8**	15 vs. 2	33.6 ± 3.8**	13 vs. 7
	vs. 16.1 ± 3.1	13* 1*	vs. 28.9 ± 3.3	1* 0
P/N vs. N/N	12.3 ± 2.6	5 vs. 12	22.6 ± 2.8	13 vs. 7
	vs. 13.4 ± 2.7	1* 2*	vs. 19.0 ± 3.2	4* 1*

Population firing rate (in spikes per second; columns 2 and 4) and cell counts (columns 3 and 5) from parietal reach region (PRR; $n = 17$) and lateral intraparietal area (LIP; $n = 20$) showing responses to first or second flashes instructing movements of a preferred (P) or nonpreferred type (N). In PRR, reaches were preferred, whereas in LIP, saccades were preferred. This held for responses to both first (row 1) and second (row 2) responses. The next two rows compare second vs. first flash responses, where each instructed the same preferred movement but the second flash either countermanded (row 3) or affirmed (row 4) the first flash. The final two rows compare the response to a countermanding vs. affirming second flash, instructing either a preferred (row 5) or nonpreferred (row 6) movement. Population data show means \pm SE under each condition with ** $P \leq 0.01$. First line of single cell data shows the number of cells in which first condition responses were greater than second condition responses vs. the number in which the second responses were greater than first. The next two lines show the number of cells for which these two inequalities were significant at $P < 0.05$ (*), respectively. See text for details.

the second compared with the first flash. The two explanations (rebound from inhibition or filtering out of superfluous information) are not mutually exclusive, and both are consistent with a role of LIP and PRR in establishing and changing motor plans.

Temporal properties of LIP and PRR responses were not identical. In this data set, large, brisk transients were common in LIP, whereas sustained responses were more common in PRR. Response latencies to first and second flashes differed by ~ 150 ms in PRR but were similar in LIP. These properties could be interpreted to suggest that LIP may be more closely related to the visual event, and PRR to the intended reaching movement. However, many PRR neurons have brisk transient responses, whereas many LIP neurons have been shown in previous studies to have long sustained activity (Gnadt and Andersen 1988; Snyder et al. 1997). Furthermore, intention affected even the earliest transient responses in some cells in both regions (Snyder et al. 1997; unpublished observations). Finally, the principal findings—selective response to flashes that shift motor intention but not attention and differential responses dependent on whether motor intention is countermanded or affirmed—occurred in both PRR and LIP. Keeping in mind that PRR may comprise more than one anatomically distinct area, perhaps each playing a different role in the visual-motor transformation, the evidence suggests that both LIP and PRR process visual information for the purpose of specific motor planning.

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