

Saccade-Related Activity in the Parietal Reach Region

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Snyder, Lawrence H., Aaron P. Batista, and Richard A. Andersen. Saccade-related activity in the parietal reach region. *J. Neurophysiol.* 83: 1099–1102, 2000. In previous experiments, we showed that cells in the parietal reach region (PRR) in monkey posterior parietal cortex code intended reaching movements in an eye-centered frame of reference. These cells are more active when an arm compared with an eye movement is being planned. Despite this clear preference for arm movements, we now report that PRR neurons also fire around the time of a saccade. Of 206 cells tested, 29% had perisaccadic activity in a delayed-saccade task. Two findings indicate that saccade-related activity does not reflect saccade planning or execution. First, activity is often peri- or postsaccadic but seldom presaccadic. Second, cells with saccade-related activity were no more likely to show strong saccadic delay period activity than cells without saccade-related activity. These findings indicate that PRR cells do not take part in saccade planning. Instead, the saccade-related activity in PRR may reflect cross-coupling between reach and saccade pathways that may be used to facilitate eye-hand coordination. Alternatively, saccade-related activity may reflect eye position information that could be used to maintain an eye-centered representation of intended reach targets across eye movements.

INTRODUCTION

Recent evidence suggests that the parietal reach region (PRR) in the medial portion of the posterior parietal cortex of the monkey reflects the planning of a reach movement. Activity related to arm movements has been recorded in these medial areas (e.g., Ferraina et al. 1997; Galletti et al. 1997; Snyder et al. 1997), and these areas project to dorsal premotor cortex, which codes reaching movements (Blatt et al. 1990; Boussaoud et al. 1998; Johnson et al. 1996; Mushiaki et al. 1997; Shipp et al. 1998; Tanne et al. 1995). PRR is activated when a reach is planned, and this activity continues until the reach is executed (Snyder et al. 1997). The activity is not sensory-specific: activity precedes reaches to both visual and auditory targets (Cohen and Andersen 1998). The activity is motor specific: when an eye movement is planned to a memorized location, activity is absent or significantly reduced during the memory period (Snyder et al. 1997). Surprisingly, reach delay activity codes the impending arm movement with respect to the eye (Batista et al. 1999). We now report that some reach-selective cells in PRR are also active during or just after saccadic eye movements.

METHODS

A square array of nine buttons (3.7 cm) containing red and green light-emitting diodes (LEDs) were placed 28 cm from rhesus monkeys

trained to look at red buttons and to press green buttons. Eye position and button presses were recorded with 2-ms resolution. Extracellular potentials were recorded using tungsten electrodes inserted daily through the medial, posterior quadrant of 19 mm (diameter) chambers mounted flush to the skull and centered at 5–6 mm posterior and 12–13 mm lateral (Horsley-Clarke coordinates). Activity from 206 isolated units from three adult animals was recorded during interleaved delayed saccade and delayed reach trials. [This included data from 131 cells from 2 animals used in previous studies (Snyder et al. 1997, 1998)]. Both tasks began with fixation and depression of the illuminated central button. After 750 ms, one of eight red (saccade task) or green (reach task) peripheral LEDs was flashed for 150 or 300 ms. After a 0.8- to 1.6-s delay period, the central button was extinguished and the animal made an eye or arm movement (not both) in complete darkness to the remembered flash location. Eight trials of each type were performed.

Neuronal activity was measured in several intervals. Delay activity was measured 150–600 ms after peripheral flash offset on both delayed saccade and delayed reach trials. Perisaccadic activity was measured 40 ms before to 80 ms after the time of peak eye velocity. Pre- and postsaccadic activities were measured 190–40 ms before and 80–280 ms after the time of peak eye velocity, respectively. To minimize contamination of these saccadic measurements by delay period activity, activity in an equal-sized interval ending 250 ms before the start of the measured interval was subtracted from pre-, peri-, and postsaccadic measurements. An ANOVA ($P < 0.05$) then was performed to detect significant effects of direction on firing rate during the delay and saccade epochs. The results we present did not depend on our specific choices of intervals; for example, similar results were obtained when cue activity (50 ms before to 150 ms after flash offset) was used instead of delay period activity and when saccadic measures were aligned using the start or end of the saccade rather than peak velocity.

RESULTS

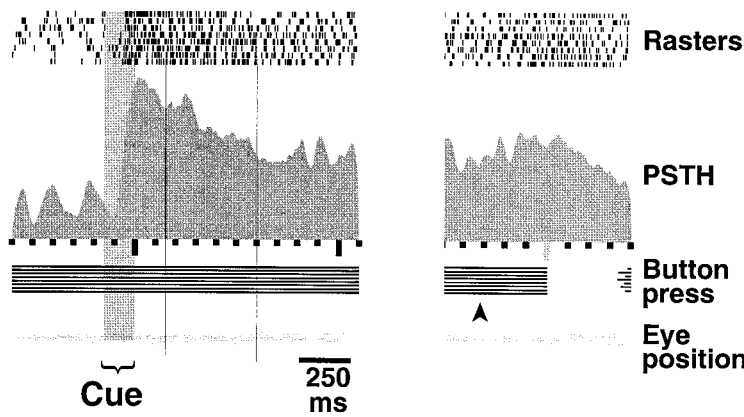
PRR cells were strongly selective for arm compared with eye movements (Snyder et al. 1997) (Figs. 1 and 2). Figure 1 shows data from one neuron. A green or red target flash (shaded rectangles on *left*) instructed the animal to prepare either a reach (*A*) or a saccade (*B*). Green and red flashes occurred at identical locations in space. Green flashes elicited a large and sustained response, while red flashes elicited a smaller, transient response (*left*). Thus the cell was active during the 1-s delay period between cue and response only if a reach was being planned.

Despite a strong preference for coding intended reaches over intended saccades, this neuron showed saccade-related discharge. Firing increased at the time of saccade initiation in the delayed saccade task (*B, right*). In this cell, activity began in the perisaccadic interval and continued through the postsaccadic interval.

The presence or absence of saccade-related activity was not predictive of the relative strengths of saccadic and reach delay

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A DELAYED REACH TASK



B DELAYED SACCADE TASK

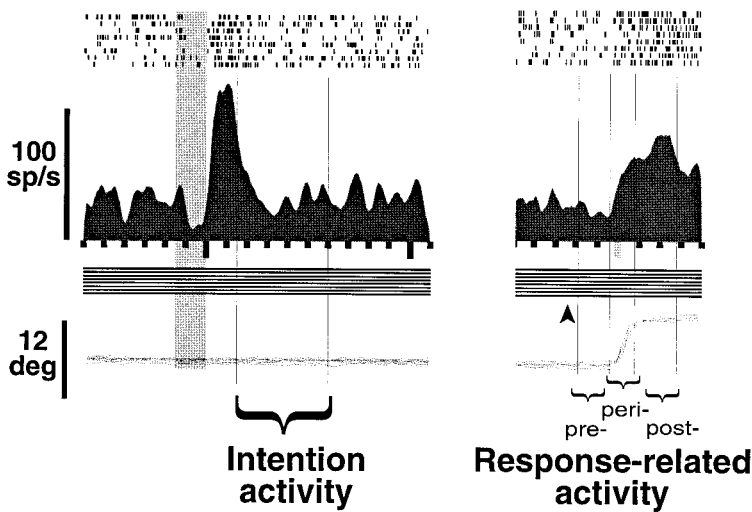


FIG. 1. Responses from 1 cell in delayed reach (A) and delayed saccade (B) paradigms. Delay activity was strongly selective for reaches, yet there was a burst of activity with each saccade. *Left*: panels are aligned on cue presentation (gray rectangle). *Right*: panels are aligned on center button release or peak saccade velocity (A and B, gray tics). Each panel contains rasters, a peristimulus time histogram, horizontal eye position and button push records for all 8 trials. Vertical lines bracket the intervals used to measure intention activity (A) and pre-, peri-, and postsaccade related activity (B). Upward arrowheads indicate the mean time of fixation point offset, the signal to initiate the delayed movement (*right*).

activity. A strong correlation might occur if a subset of cells coded plans for saccadic eye movements, as in the lateral intraparietal area (Snyder et al. 1997). However, this was not

the case. Of 206 cells recorded in PRR, 59 had significant perisaccadic activity (40 ms before to 80 ms after peak eye velocity). Of these, 50 also had significant delay period activity

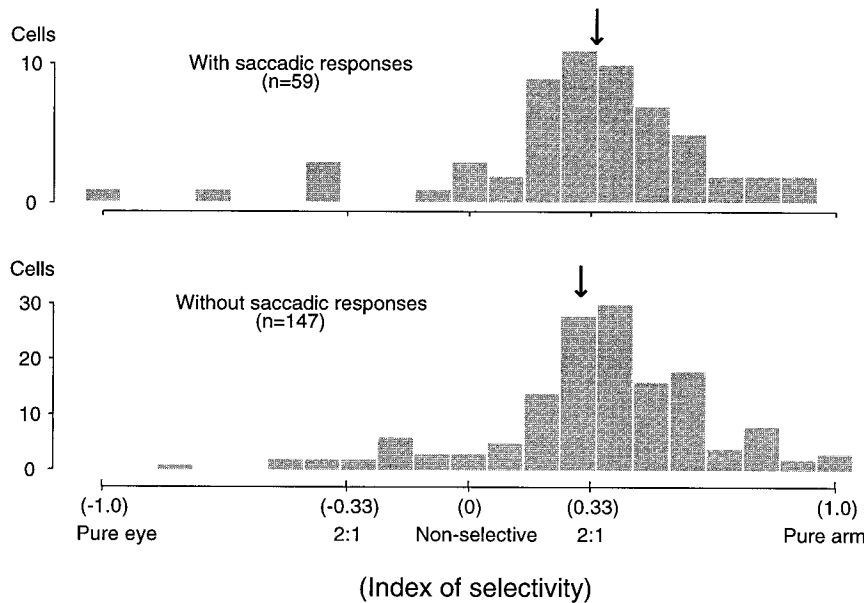


FIG. 2. Delay activity of parietal reach region (PRR) cells either with (*top*) or without (*bottom*) saccadic responses. Most cells were more active when a reach was being planned than when a saccade was being planned. Index of selectivity (*x* axis) captures whether cells are more active 150–600 ms after a cue instructs a delayed saccade or a delayed reach (see text). Cells selective for planned eye movements fall on the left (“Pure eye”), cells selective for planned arm movements fall on the right (“Pure arm”), and nonselective cells fall in the middle (“Nonselective”). Intermediate tic marks indicate cells with a 2:1 ratio of activity in the 2 tasks. Distributions of indices for cells with and without perisaccadic responses are similar with nearly identical mean values (\downarrow).

before a reach. In 53 of 59 cells, delay activity was stronger before a reach than before a saccade. Only 6 of 59 cells showed the reverse effect. These differences were significant in 37 and 5 cells, respectively. Thus even within the subset of PRR cells active during a saccade, the overwhelming majority were more active when a reach compared with a saccade was being planned.

Figure 2 compares motor intention selectivity for PRR cells with (*top*) and without (*bottom*) presaccadic activity. An index of motor intention was calculated as $(arm - eye)/(arm + eye)$, where *arm* was mean firing in the delayed reach task, and *eye* was mean firing in the delayed saccade task, measured 150–600 ms after flash offset and well before the actual movement. The index could vary from -1 (selective for saccadic eye movements) to $+1$ (selective for arm movements). Cells with and without saccade-related activity had similar index values (mean values 0.31 and 0.35; not significantly different by Student's *t*-test). Thus the presence or absence of presaccadic activity was independent of the degree to which cells were differentially active in the delay period preceding arm movements or saccades.

Fifty-nine of 206 cells (29%) had significant presaccadic modulation, and 70 (34%) had significant postsaccadic modulation (ANOVA, $P < 0.05$). In contrast, only 14 (7%) had significant presaccadic modulation. Fourteen of 206 cells is not significantly greater than the expected 5% false positive rate (χ^2 test, $P > 0.15$).

Presaccadic activity was tuned in the same direction as intended reach activity (Fig. 3). We plotted the difference between preferred directions for presaccadic and reach delay period activity for the 50 cells that showed both effects. Preferred directions were identified by the direction of eye movement or intended arm movement resulting in the maximal response. The vector sum of the angles representing the difference between preferred directions had an orientation of -1.2° and was highly significant (circular statistics, $P < 0.0001$, Fisher 1993). Thus the preferred directions of reach intention activity and presaccadic activity were aligned.

If presaccadic activity reflected participation in saccade planning, we would expect presaccadic activity to be more

closely aligned with saccade delay activity than with reach delay activity. Instead, presaccadic activity was less well aligned with saccade delay activity than with reach delay activity [data not shown: vector sum of the difference between preferred directions of 75° for the 28 cells that showed both presaccadic and saccade delay activity, $P > 0.20$ (not significantly different from a uniform distribution)]. Similarly, if presaccadic activity reflected participation in saccade planning, we also would expect that the breadth of tuning of presaccadic activity would more closely resemble the breadth of tuning of saccade delay activity than reach delay activity. Once again, the reverse was true. The correlation of median width at half-height between presaccadic activity and saccade delay activity was only 0.01 (Pearson coefficient; $P > 0.2$), whereas the correlation between presaccadic activity and reach delay activity was 0.34 ($P < 0.05$).

DISCUSSION

Reach responses have been previously described in parietal cortex (e.g., Ferraina et al. 1997; Galletti et al. 1997; Hyvarinen et al. 1974; Mountcastle et al. 1975; Snyder et al. 1997). Because primates often couple their eye and arm movements to visual targets (Ballard et al. 1992), it is important to distinguish between visually evoked, reach-related, and saccade-related activity. In the current study, we used delayed saccade and reach trials to show that neurons in PRR the activity of which is related to planning a reaching movement are also active at the time of a saccade.

Data from delayed movement trials shows that cells in PRR are selective for intended reaching movements. Cells are less active when the animal plans a saccade compared with a reach (Figs. 1 and 2). This selectivity is even greater when a saccade and a reach are planned at the same time but in opposite directions (Snyder et al. 1997). Despite this clear selectivity for reaching movements, one-third of PRR cells also were activated during or just after a saccade (e.g., Fig. 1).

One interpretation of these data is that PRR contributes to saccade planning or execution. However, several lines of evidence refute this idea. First, few PRR cells show presaccadic activity. This contrasts with findings from the lateral intraparietal area (LIP), where cells are active while a saccade is being planned and also in the presaccadic interval (Barash et al. 1991; Snyder et al. 1997). Second, one would expect that if cells with saccadic activity are involved in saccade planning and execution, then these cells would be more active when a saccade compared with a reach is being planned. This was not the case; PRR cells with and without saccade-related activity were overwhelmingly reach selective, with no significant difference between the two groups (Fig. 2). Finally, the preferred directions of saccade activity were closely aligned with the preferred directions of reach delay period activity (Fig. 3) but not with the preferred directions of saccade delay period activity. Exactly the reverse pattern would be expected if presaccadic and saccade delay activity was involved in coding intended saccades.

A second interpretation of these data is that whenever the eyes are moved, a plan is formed in PRR that would carry the arm to the same target. On delayed saccade trials, this plan then is suppressed somewhere between PRR and the motor output. In this view, the activity in PRR during a saccade is a mani-

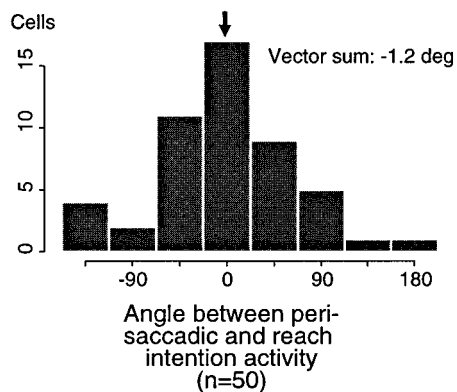


FIG. 3. Best directions for evoking presaccadic activity are aligned with the best directions for evoking reach delay period activity. Histogram shows the number of cells with particular angles between the direction evoking the best presaccadic response and the best reach delay period response. Vector sum of the angles is -1.2° (\downarrow), indicating that the directional tuning for presaccadic and reach intention activity is aligned. Only cells with significant saccadic and reach intention activity are included.

festation of cross-coupling between reach and saccade pathways. A similar explanation was proposed to explain the small amount of activity that occurs in PRR in the delay interval before a saccade, and the small amount of activity that occurs in LIP in the delay interval before an arm movement (Snyder et al. 1997). Cross-couplings between two sensory-motor transformation pathways have been described previously in other motor systems (Mays and Gamlin 1995). In PRR, cross-coupling between eye and arm movement responses could reflect a neural substrate for eye-hand coordination.

A third interpretation of these data is that saccadic signals in PRR are used to maintain an eye-centered representation of the goal of an intended reach. Many PRR cells code the goal location for an intended reach with respect to the direction of gaze (Batista et al. 1999; Cohen and Andersen 1998). If the eyes move after a target appears but before a reach is made, the pattern of activity in PRR changes to maintain target location in an eye-centered frame of reference. The necessary computation could be performed in PRR, using corollary discharge of eye movement commands (Zeki 1986).

To maintain an eye-centered representation of target location, vectors representing eye movements would need to be subtracted from vectors representing intended reach targets. We might have expected that an efficient algorithm would code eye movements and target locations using opposed rather than aligned preferred directions, given that these vectors must be subtracted, but this was not what we observed (Fig. 3). Further work is required to determine which of these last two interpretations of saccade-related activity in PRR is correct.

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