

The Parietal Reach Region Codes the Next Planned Movement in a Sequential Reach Task

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Batista, Aaron P. and Richard A. Andersen. The parietal reach region codes the next planned movement in a sequential reach task. *J Neurophysiol* 85: 539–544, 2001. Distinct subregions of the posterior parietal cortex contribute to planning different movements. The parietal reach region (PRR) is active during the delay period of a memory-guided reach task but generally not active during a memory-guided saccade task. We explored whether the reach planning activity in PRR is related to remembering targets for reaches or if it is related to specifying the reach that the monkey is about to perform. Monkeys were required to remember two target locations and then reach to them in sequence. Before the movements were executed, PRR neurons predominantly represented the reach about to be performed and only rarely represented the remembered target for the second reach. This indicates the area plays a role in specifying the target for the impending reach and may not contribute to storing the memory of subsequent reach targets.

INTRODUCTION

When interacting with its surroundings, an animal must continually monitor the environment and plan and execute actions tailored to the current situation. Complex real-world circumstances demand that animals select from a range of possible actions, coordinate the movements of several body parts, and plan several actions into the future. An important goal in neurophysiology is to understand how the brain performs the various tasks involved in planning and executing movements.

In a recent study, we showed that the posterior parietal cortex (PPC) of monkeys contains distinct subregions that process different types of movements (Snyder et al. 1997). In that study, monkeys performed memory-guided saccadic eye movements and memory-guided reaches. We found that the lateral intraparietal area (LIP) is active when the animal plans to make a saccade. A nearby area, the parietal reach region (PRR), is active when the animal plans to reach.

While an animal is planning a reach to a remembered location, several processes are engaged. The location of the target must be held in memory, and the reach to that location must be prepared. Neural signals in PRR preceding a reach to a remembered location could be related to either of these processes or both. To dissociate these processes, we exploited the facts that several memories can be stored simultaneously, but move-

ments must be planned in series because a particular body part can only be moved to one location at a time. We trained monkeys to perform sequential reaches to remembered targets. After both targets have been presented and before either reach has been performed, the monkey must remember both targets, and prepare the first reach. Neural signals in PRR might encode both reach targets the monkey is storing in memory. Alternatively, PRR may represent only the target toward which the animal is currently planning to reach, consistent with a role for PRR in planning the impending movement.

A brief report of these findings has appeared (Batista et al. 1998).

METHODS

Animals, surgery, and experimental apparatus

Three adult male monkeys (*Macaca mulatta*; designated *D*, *G*, and *O*) were studied in this experiment. Procedures were in accordance with the guidelines of Caltech's Institutional Animal Care and Use Committee. Under pentobarbital anesthetic, a head holder and eye coil (Judge et al. 1980) were implanted. After training, a second surgery was performed to implant a recording cylinder over areas LIP and PRR. During recording sessions, the animal's head was braced, and a microelectrode was lowered into PRR. Single neurons were isolated using a dual-window discriminator (BAK Electronics, Germantown, MD). All three animals are still involved in experiments, so our definition of PRR is based on the functional criteria of greater reach planning activity than saccade planning activity and the fact the area occupies a region of the brain just medial and caudal to LIP (Batista et al. 1999; Snyder et al. 1997). Animals sat in a dark room facing a vertically positioned array of touch-sensitive buttons 24 cm away. Buttons were spaced 18° in the array. Each button was 3.7 cm in diameter and contained a red and a green light-emitting diode (LED) behind a translucent window 1.2 cm in diameter.

Behavioral tasks

Neurons were first tested for reach selectivity and response fields (RFs) were mapped while animals performed delayed reach (DR) and delayed saccade (DS) tasks (Batista et al. 1999; Snyder et al. 1997). The arm contralateral to the recording site was used. A red and a green LED were illuminated at the center button of the array, signaling the animal to look at and press that button. Five hundred milliseconds later, either a red or a green cue would appear for 300 ms at one of the

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eight buttons surrounding the center button. An 800-ms delay period ensued, which was terminated by extinguishing both central LEDs as a go signal. Then if the cue had been red, the animal would saccade (without moving its hand) to the location where it had appeared; if the cue had been green, the animal would reach to its location (without making a saccade). After holding the final position for 600 ms, a juice reward was delivered. A neuron was deemed reach selective if its maximal response (across all 8 targets) during the delay period of the DR task was significantly greater (Mann-Whitney test, $P < 0.05$) than its maximal delay-period response in the DS task. Only neurons reach selective by this criterion were analyzed in the current experiment.

After neurons were screened in this manner, monkeys performed interleaved trials of a DR task and an intervening reach (IR) task (Fig. 1). The IR task was a variant of the DR task where, 600 ms into the delay period following the presentation of the first cue, a second cue was presented. The first cue was chosen to be in the RF of the cell (this cue is termed c_{in}), and the second was outside the RF (c_{out}). Another 600 ms of delay period ensued before the go signal. (The delay period following the 1st cue is termed $d1$, and $d2$ is the delay following the 2nd cue.) When the central LEDs were extinguished, the animal reached (without moving its eyes) to the location where c_{out} had been presented (the 1st reach is termed r_{out}). On completion of the reach, the central red LED and the green LED at the button the monkey was currently pressing were reilluminated, and a third delay period ($d3$) occurred for 500 ms. Both LEDs were again extinguished as the second go signal, and the animal reached to the location where the first cue had been presented (r_{in}), again without breaking fixation at the central button. Conceptually, in this task, c_{in} instructs a reach which is eventually executed, but a delayed reach to c_{out} intervenes between the presentation of c_{in} and the reach to it.

The interleaved trials of the DR task were modified so that the delay period (d) was lengthened, typically to 1,100–1,500 ms. Also, in the DR task the cue would appear at one of only two locations, either c_{in} or c_{out} . The overall structure of the task was that on half of the trials when c_{in} appeared, the monkey would reach to it after the delay period (DR trials). For the other half of the trials when c_{in} appeared, the delay period would be interrupted by the appearance of c_{out} , and the monkey would be required to perform r_{out} before r_{in} (IR trials).

During neural recording, the positions of c_{in} and c_{out} were fixed throughout the test of an individual neuron. Typically, 10 trials of each of the three types (DR tasks to c_{in} and c_{out} , and IR task) were performed. Animals generally performed over 90% correct; animals almost never mistakenly executed the first reach in the IR task to c_{in} .

An additional target configuration was tested for some neurons: the order of cues in the IR task, and thus the order of reaches, was reversed. c_{out} was presented first, and c_{in} appeared second. The monkey performed r_{in} , then r_{out} .

Fixation was maintained throughout each trial within a square window 5° on a side for *monkeys D* and *O* and within a rectangular window 5° horizontal by 12° vertical for *monkey G*. The larger window was needed to accommodate an upward drift in eye position during the delay period. This drift was present in all trials and was not related to target position.

Analysis

A one-tailed Mann-Whitney test (nonparametric t -test) at the $P < 0.05$ level was used for all comparisons of neural activity. The epochs used were as follows. In the IR task, $d1$ was measured as the 500-ms interval starting 100 ms after c_{in} was extinguished and extending to the time c_{out} appeared, $d2$ was the 500-ms epoch from 100 ms after the offset of c_{out} until the first go signal, and $d3$ was the 400-ms interval from 100 ms after the monkey touched the location of c_{out} until the second go signal. In the DR task, the final 500 ms of the d epoch (preceding the go signal) was used. In all statistical comparisons, the same duration is used for both epochs in the comparison. Thus for the comparisons to $d3$, the d , $d1$, and $d2$ epochs were shortened to 400 ms.

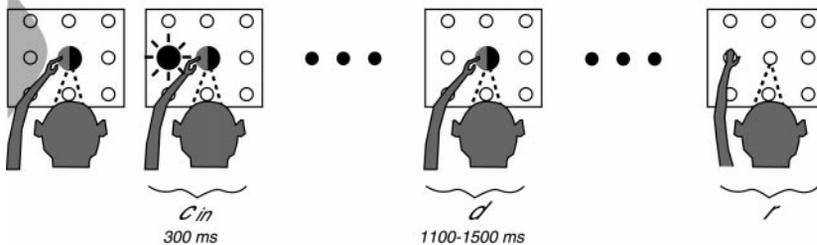
Neurons were screened to ensure that c_{in} and c_{out} were indeed in and out of the RF, respectively. The firing rate during the d epoch of the DR task was compared for reaches to each target. Only if the response for reach plans to c_{in} was significantly greater than the response for reach plans to c_{out} were data from the IR task analyzed.

To quantify the behavior of each neuron in response to the appearance of c_{out} , an index was computed

$$\text{Index} = \frac{\text{DR}_{out} - \text{IR}}{\text{DR}_{out} - \text{DR}_{in}}$$

where DR_{out} is the mean firing rate during the d epoch of the DR task when the target is presented out of the RF, DR_{in} is the firing rate in the DR task when the target is in the RF, and IR is the firing rate during the $d2$ epoch of the IR task. An index near 1 indicates that the cell is unaffected by the appearance of c_{out} , while an index near 0 indicates that the cell's response after c_{out} drops to a level near its response during the DR task when the target is presented out of the RF. To establish a baseline, this index was also computed using the $d1$

Delayed Reach (DR) task



Intervening Reach (IR) task

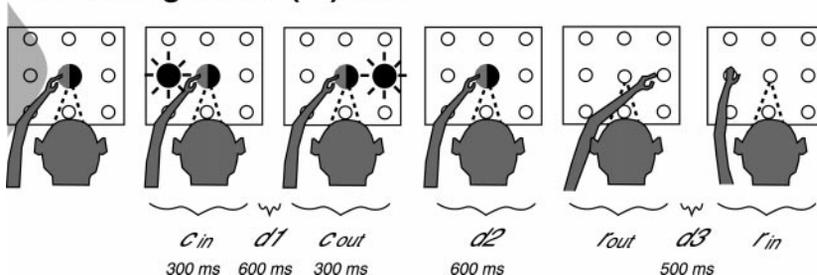


FIG. 1. The delayed reach (DR) task (*top*) and intervening reach (IR) task (*bottom*). Each panel shows a behind-the-head view of the monkey and the button array. Below the panels are the names and durations of the task epochs. An example response field (RF) location is shaded gray in the 1st panel of each row. The monkey begins the trial by fixating and pressing the central button, where a red light-emitting diode (LED, shown as gray) and green LED (shown as black) have been illuminated. In the DR task configuration pictured, a cue is presented in the RF (c_{in}). A delay period (d) ensues before the center LEDs are extinguished to trigger the reach (r). In the IR task, c_{in} is followed by a delay period ($d1$, not pictured), then a cue is presented out of the RF (c_{out}). Another delay period ($d2$) follows. After the go signal, the animal reaches to the location of c_{out} (r_{out}). A 3rd delay period ensues ($d3$, not pictured) before the monkey is instructed to reach to the location of c_{in} (r_{in}). Two other trial types are not shown: the DR task where c_{out} is presented, and the IR task with the order of c_{in} and c_{out} reversed.

interval in the IR task and the early portion of the delay interval (from 100 to 600 ms after cue offset) in the DR task. This index is expected to be near 1.

RESULTS

In the IR task, the first cue (c_{in}) was positioned in the RF, so it activated the neuron. When the second cue (c_{out}) appeared, it was positioned outside of the RF. The monkey was required to shift its reach plan to that location because the first reach would now be directed there. What effect would the appearance of c_{out} have on the sustained activity due to the presentation of c_{in} ? The monkey must hold in memory the location where c_{in} was presented because he will eventually reach to it. PRR may contribute to remembering that target, in which case the response elicited by c_{in} would not be affected by the appearance of c_{out} . Alternatively, it could be that PRR specifies only the movement about to be performed and does not retain the memory of targets for subsequent movements. In this case, the activity elicited by c_{in} should diminish as the monkey shifts its plan for the impending reach to the location of c_{out} .

Figure 2 shows one neuron studied in this experiment. Figure 2A shows the responses during the DR task for reaches into (*left*) and out of (*right*) the RF. Figure 2B shows the response during the IR task, where the first cue appears in the RF and the second is outside of the RF. The appearance of c_{in} elevated the firing rate of the neuron. As c_{out} appeared and the monkey shifted its reach plan to the target out of the RF, the activity of the neuron was curtailed. Once r_{out} was performed, the monkey resumed planning the reach to the location of c_{in} . Correspondingly, activity resumed in this cell. The pattern of discharge in this cell is consistent with a representation of the next planned movement in PRR and is inconsistent with the hypothesis that PRR stores the targets for all planned reaches simultaneously.

Most neurons (14 of 14 tested in *monkey D*, 13 of 13 tested in *monkey O*, and 3 of 7 tested in *monkey G*) dropped significantly in mean firing rate when the second cue was presented ($d2$ activity significantly less than d activity, Mann-Whitney test, $P < 0.05$). An index (described in METHODS) was computed for each neuron to quantify these effects for the population of PRR neurons (Fig. 3A). Index values cluster around 0, indicating that, after c_{out} appears, neurons are about as active as they are on trials when only one reach is planned, out of the RF. Although the monkey must remember the location of c_{in} until the second reach is performed, overall PRR does not store that plan. To establish a baseline for the population plot of Fig. 3A, this analysis was repeated on the $d1$ interval of the IR task (see METHODS). The histogram of indices is shown in Fig. 3B. Only one neuron showed a significantly different response during this epoch between the IR task and the DR task configuration with the target in the RF.

Figure 4 shows one of the four neurons that behaved differently: this cell continued to signal c_{in} after the presentation of c_{out} . It is thus more consistent with a role in holding the memory of target locations because it cannot contribute to an unambiguous specification of the impending reach. All four of these neurons were collected from *monkey G*. It is possible that PRR contains a subregion where neurons are involved in maintaining the memory of reach targets and that our recordings in *monkeys D* and *O* missed this subregion. However, we

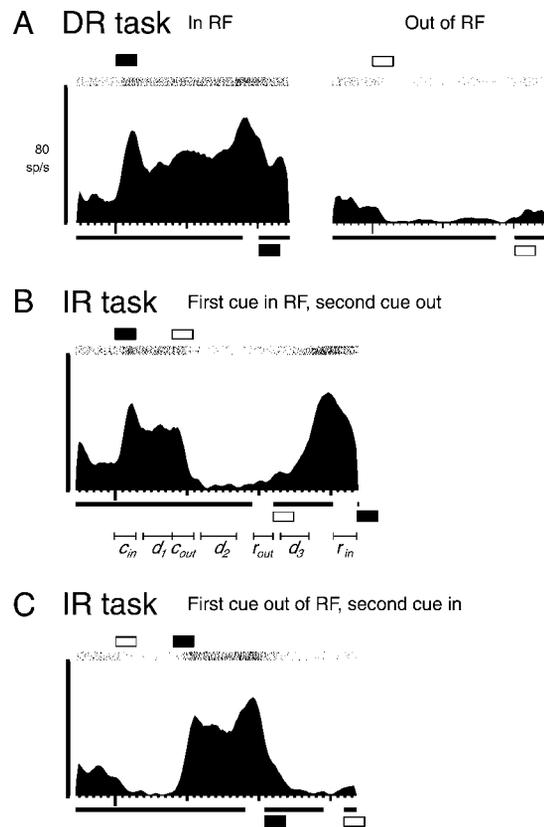


FIG. 2. Behavior of 1 parietal reach region (PRR) neuron tested in the target selection experiment. A–C: each subplot shows, from top to bottom: timing of cue presentation, where a filled bar represents a cue in the RF, and an open bar represents a cue out of the RF; spike rasters for 10 repetitions of the movement; spike density function constructed from those rasters, using a triangular kernel (Scott 1985); the timing of button presses for one representative trial; the symbols below this trace indicate which target was acquired, where an open symbol represents a reach to a target out of the RF and a filled symbol represents a target within the RF. The final row in B shows the timings of the epochs of the IR task. Tic marks, 100 ms. A: the DR task performed to a target in the RF (*left*) and out of the RF (*right*). B: the IR task where the 1st cue is presented in the RF, and the 2nd is presented outside. This neuron had an index of 0.03 (Fig. 3A). C: the IR task where the 1st cue is presented out of the RF and the 2nd is in the RF.

curtailed recording from *monkey G* because single neurons were much more difficult to isolate, probably due to the extensive recording from PRR that had been performed during a prior study. It could be that the prolonged recording induced differences in the neurons' response properties. Even in light of this consideration, it remains an open possibility that there are different populations of neurons in PRR: the majority representing the impending reach and a minority storing the memory of targets for eventual reaches.

Once the first reach is executed, the animal is required to resume planning a reach into the RF. Accordingly, in Fig. 2B, activity returns to the neuron during $d3$. This was evident in most cells: 26 of the 34 neurons showed a significantly greater response during $d3$ than during $d2$ (Mann-Whitney test, $P < 0.05$). The average response during $d3$ was 3.03 times the response during $d2$ (with a range of 0.18–13.72).

Responses during $d3$ were often indistinguishable from responses during $d1$. Eighteen of 34 cells show no significant difference (Mann-Whitney test, $P < 0.05$) between the $d3$ and

d1 epochs. The mean ratio of *d3* to *d1* activity was 0.97, with a range of 0.02–1.90.

The effects reported so far are consistent with the hypothesis that PRR represents the impending reach only. However, also consistent with these data is the possibility that PRR does not represent any reach plan at all after the second cue appears. To ensure that PRR indeed specifies the first reach during the IR task, we reversed the order of cue presentations: c_{out} was presented first, followed by c_{in} . This instructed the monkey to reach into the RF first and out of the RF subsequently. Figure 2C shows data from a neuron tested in this task. The appearance of the first cue does not activate the neuron because it falls out of the RF. However, the second cue does activate the neuron as the animal plans a reach into the RF. After that reach, the neuron falls silent, as the animal is required to resume planning a reach out of the RF, to the location of the first cue. We tested five neurons from *monkey D* in this manner. All five cells showed a significant increase in activity when the second cue was presented in the RF compared with the cell's response during the equivalent time period in the DR task when the sole target was out of the RF (Mann-Whitney test, $P < 0.05$). All five neurons also dropped in activity during *d3*, once the first reach was completed and the monkey resumed planning a reach to a target out of the RF (response during *d3* significantly less than response during *d2*, Mann-Whitney test, $P < 0.05$).

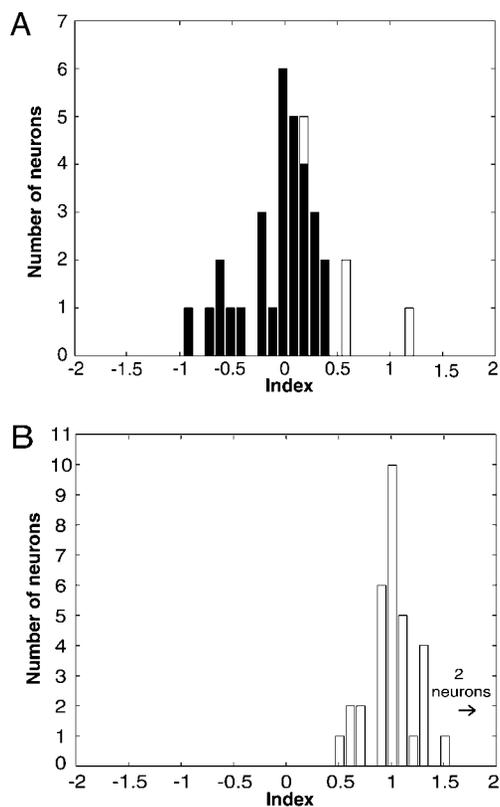


FIG. 3. *A*: histogram of indices (see METHODS) for the population of PRR neurons tested in the intervening reach task. An index value of 0 represents an offset of activity in response to the appearance of c_{out} . An index of 1 indicates the appearance of c_{out} had no effect on the firing rate. ■, neurons that exhibited significant decreases in activity in response to c_{out} . □, neurons without a significant drop in activity. *B*: histogram of indices computed during the *d1* interval of the IR task. □, neurons that exhibit no significant difference in firing rate between the DR task and the *d1* period of the IR task. One neuron (index = 2.8) did show a significant difference.

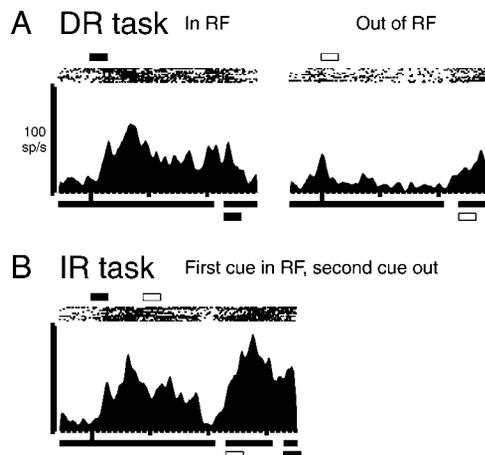


FIG. 4. A PRR neuron that may contribute to storing the second reach plan. Subplots are as described in Fig. 2 caption. *A*: behavior of the neuron in the DR task for a target in the RF (*left*) and out of the RF (*right*). *B*: behavior of the neuron in the IR task. This neuron had an index of 1.2 (Fig. 3A).

Thus these PRR neurons were active when and only when the impending reach was planned into the RF. Interestingly, activity during *d1* and *d3* was distinguishable, with *d3* responses 4.3 times greater than *d1* responses, on average (range from 2.1 to 9.0).

DISCUSSION

Animals were required to remember the locations of two briefly presented visual targets, and reach to them in sequence. Eighty-eight percent of the 34 PRR neurons tested ceased to represent a target location once it became the target for a subsequent reach and not the impending reach. This is consistent with the hypothesis that PRR is involved in specifying the target for the impending reach and is less involved in storing the memory of reach targets. The pattern of activity in PRR changes as the reach plan shifts so that the active population of neurons always represents the direction of the impending reach.

A strong prediction of the present findings is that if animals are presented with a free-choice task where they are free to reach to one of several targets to receive a reward, neurons in PRR will again represent only the movement the animal selects and not all possible reaches under consideration. We believe that signals in PRR reflect the outcome of a process of target selection for reaches. Moreover the activity is specific for the target selected for the impending movement not a subsequent movement.

The performance of a goal-directed movement can be viewed as composed of three processes: a type of action must be chosen (the situation may require simply looking around a scene, or it may be that an object must be approached, or picked up); a target must be selected (natural environments offer many possible objects on which to act at any time); and the brain must convert the sensory representation of the object selected into a coordinated pattern of muscular activity so that the chosen movement can be performed. These components of sensory-motor processing offer a useful framework for synthesizing the observations made in several recent studies of PPC.

Different types of movement are planned in distinct regions of PPC (Snyder et al. 1997). PRR is involved in planning

reaches but not saccades, while nearby area LIP represents plans for eye movements and not reaches. Thus signals in PPC reflect the outcome of the process of choosing a type of movement.

In a recent study, area LIP was shown to reflect the outcome of the process of target selection for saccades (Mazzoni et al. 1996). Most neurons in LIP were found to be active only when the impending saccade was planned into the neuron's RF; most cells were not active if a subsequent saccade was planned into the RF. The present report establishes that PRR shares this property for reaches.

Taken together, these studies present a detailed picture of the role of PPC in sensory-motor processing. Since signals in PPC reflect both the choice of a type of movement and the selection of the impending target for that movement, it can be said that these signals reflect movement intentions.

PRR has recently been shown to represent targets for reaches in eye-centered coordinates (Batista et al. 1999). Thus the area occupies a stage in neural processing antecedent to the transformation to limb coordinates. Similarly, area LIP employs eye-centered coordinates to represent targets for saccades (Colby et al. 1995; Gnadt and Andersen 1998). Both areas update their eye-centered representations of the movement plan to compensate for intervening saccades (Batista et al. 1999; Duhamel et al. 1992; Gnadt and Andersen 1998).

Although PRR reflects the outcome of the processes of target selection and movement choice, targets are represented in eye-centered coordinates in PRR. These studies converge to suggest that many stages in the planning of arm movements are performed in visual coordinates with the transformation to limb coordinates occurring quite late in sensory-motor processing.

Involvement of other cortical reach areas

Parietal cortex, including areas MIP and V6A, the likely substrata of PRR, is densely interconnected with premotor areas in the frontal lobe (Johnson et al. 1996; Matelli et al. 1998). These areas are likely to work in conjunction to perform tasks such as selecting targets for a reach, planning sequences of reaches, and converting from eye-centered to limb-centered coordinates. Like PRR, premotor cortex encodes remembered visual objects (Graziano et al. 1997). In a target-selection task (Cisek and Kalaska 1999), when two potential reach targets are presented, both are encoded in premotor cortex. When information that disambiguates the correct reach target is provided, premotor cortex signals that target alone. This provides strong evidence that in the IR task presented in this paper, the regions of premotor cortex studied by Cisek and Kalaska will likely represent only the impending reach, as does PRR. Indeed, the two areas may cooperate to create this representation.

PRR undoubtedly cooperates with other premotor areas in the performance of remembered sequential arm movements. Picard and Strick (1997) showed that the dorsal aspect of the cingulate motor area (CMAd) is preferentially activated by the performance of remembered sequences of arm movements. Tanji and Shima (1994) showed that the area just dorsal to CMAd, the supplementary motor area (SMA), is activated during the performance of remembered sequential movements. SMA neurons encode the transition from one movement to another in a sequence. We found no evidence for such a coding scheme in PRR. Instead PRR neurons seem to represent the

impending movement and, occasionally, targets for eventual reaches but were never preferentially activated by the transitions between reaches in our study (*d3* activity was indistinguishable from *d1* activity in 18 of 34 neurons). Frontal premotor areas involved in movement sequencing are likely to transmit signals of the impending reach target to PRR during sequential reach tasks.

To perform a visually guided reach, targets must be converted from eye-centered coordinates to limb-centered coordinates. This transformation is likely to involve a network of brain areas, including regions of parietal and frontal cortices. PRR represents targets in eye-centered coordinates (Batista et al. 1999) while a number of cells in the ventral aspect of premotor cortex (PMv) use a limb-centered representation (Graziano et al. 1994). Some PMv neurons are modulated by the direction of gaze (Mushiake et al. 1997), suggesting this area may contain a combination of neurons using eye- and limb-centered coordinate frames. Similarly there exist both intrinsic and extrinsic representations of reach goals in area M1 (Takei et al. 1999). PRR is likely to be part of a distributed network of brain areas involved in preparing reach movements.

Where is the second reach plan stored?

After the first cue, the monkey is given no further instruction as to the location of the target for the second reach. This information must be stored internally. However, after the second cue appears, there is only a weak trace of the memory of the first cue in PRR. After the first reach, as the monkey resumes planning a reach to the location of the first cue, that plan is again represented in PRR. Clearly other brain areas must hold the memory of the location for the second reach in between. There are of course many possible mechanisms for how this memory is stored; two are outlined here. It could be that another cortical area stores both targets with one or the other being passed to PRR according to task demands. This area could be a sensory area that sends a feedforward projection to PRR, or a premotor area, such as CMAd (Picard and Strick 1997) or SMA (Tanji and Shima 1994) that sends a feedback projection to PRR. Alternatively, perhaps neurons in a premotor area store the second reach alone (Kettner et al. 1996). This reach plan could be represented in this hypothesized premotor area in eye-centered coordinates, similar to PRR or in hand-centered coordinates (Graziano et al. 1994). If the latter is true, the signal must be back-converted into eye-centered coordinates because that is the form in which it appears in PRR. Experiments to determine the location where the second reach plan is stored, the manner in which it is represented and how it is transferred to PRR will be important to perform.

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REFERENCES

BATISTA AP, BUNEO CA, SNYDER LH, AND ANDERSEN RA. The parietal reach region (PRR) employs a predominantly retinal reference frame which up-

- dates across saccades, and encodes only the impending reach. *Soc Neurosci Abstr* 24: 262, 1998.
- BATISTA AP, BUNEO CA, SNYDER LH, AND ANDERSEN RA. Reach plans in eye-centered coordinates. *Science* 285: 257–260, 1999.
- CISEK P AND KALASKA JF. Neural correlates of multiple potential motor actions in primate premotor cortex. *Soc Neurosci Abstr* 25: 381, 1999.
- COLBY CL, DUHAMEL J-R, AND GOLDBERG ME. Oculocentric spatial representations in parietal cortex. *Cereb Cortex* 5: 470–481, 1995.
- DUHAMEL J-R, COLBY CL, AND GOLDBERG ME. The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* 255: 90–92, 1992.
- GNADT JW AND ANDERSEN RA. Memory related motor planning activity in posterior parietal cortex of macaque. *Exp Brain Res* 70: 216–220, 1988.
- GRAZIANO MSA, HU XT, AND GROSS CG. Coding the locations of objects in the dark. *Science* 277: 239–241, 1997.
- GRAZIANO MSA, YAP GS, AND GROSS CG. Coding of visual space by premotor neurons. *Science* 266: 1054–1057, 1994.
- JOHNSON PB, FERRAINA S, BIANCHI L, AND CAMINITI R. Cortical networks for visual reaching: physiological and anatomical organization of frontal and parietal lobe arm regions. *Cereb Cortex* 6: 102–119, 1996.
- JUDGE SJ, RICHMOND BJ, AND CHU FC. Implantation of magnetic search coils for measurement of eye position: an improved method. *Vision Res* 20: 535–537, 1980.
- KAKEI S, HOFFMAN DS, AND STRICK PL. Muscle and movement representations in the primary motor cortex. *Science* 285: 2136–2139, 1999.
- KETTNER R, MARCARIO J, AND PORT N. Control of remembered reaching sequences in monkey. II. Storage and preparation before movement in motor and premotor cortex. *Exp Brain Res* 112: 347–358, 1996.
- MATELLI M, GOVONI P, GALLETI C, KUTZ DF, AND LUPPINO G. Superior area 6 afferents from the superior parietal lobule in the macaque monkey. *J Comp Neurol* 402: 327–352, 1998.
- MAZZONI P, BRACEWELL RM, BARASH S, AND ANDERSEN RA. Motor intention activity in the macaque's lateral intraparietal area. I. Dissociation of motor plan from sensory memory. *J Neurophysiol* 76: 1439–1455, 1996.
- MUSHIAKE H, TANATSUGU Y, AND TANJI J. Neuronal activity in the ventral part of premotor cortex during target-reach movement is modulated by direction of gaze. *J Neurophysiol* 78: 567–571, 1997.
- PICARD N AND STRICK PL. Activation on the medial wall during remembered sequences of reaching movements in monkeys. *J Neurophysiol* 77: 2197–2201, 1997.
- SCOTT D. Averaged shifted histograms: effective nonparametric density estimators in several dimensions. *Ann Statist* 13: 1024–1040, 1985.
- SNYDER LH, BATISTA AP, AND ANDERSEN RA. Coding of intention in the posterior parietal cortex. *Nature* 386: 167–170, 1997.
- TANJI J AND SHIMA K. Role for supplementary motor area cells in planning several movements ahead. *Nature* 371: 413–416, 1994.