36 Programming to Look and Reach in the Posterior Parietal Cortex

R. A. ANDERSEN, A. P. BATISTA, L. H. SNYDER, C. A. BUNEO, AND Y. E. COHEN

ABSTRACT   Classically, the posterior parietal cortex (PPC) has been believed to be an association sensory area responsible for attention and spatial awareness. Over the past few years, however, a new idea has emerged that this area also analyzes sensory information for the purpose of planning actions. Experiments from the authors' laboratory have shown that the PPC has an anatomic map with respect to intentions. The PPC is an "association" cortex in the sense that it must combine different sensory modalities, which are coded in different coordinate frames, within this map for action plans. Interestingly, two different areas of the PPC, one involved with moving the eyes (the lateral intraparietal [LIP] area) and another involved with moving the arms (the parietal reach region [PRR]), both appear to represent the goals for movements using the same set of rules, even though the eventual outcome of their activities are for different behaviors. In both areas, individual neurons code spatial locations using a common reference frame, that is, with respect to the eye, but these responses also are gain-modulated by eye and body position signals. At the population level, this mechanism allows these areas to code concurrently a goal for movement in multiple coordinate frames (eye, head, body, and world). Depending on how this group of cells is sampled by other areas of the brain, different coordinate transformations can be accomplished by this same population of neurons.

The posterior parietal cortex generally is believed to be a high-order sensory region that contributes to spatial awareness. The phenomenon of "neglect," which results after lesions to this area, manifests as a deficit in attending to objects in the affected visual field or in shifting attention and has been used as a prime example of a sensory attention role for PPC (Critchley, 1953; Andersen, 1987, for review). However, another syndrome also common with PPC lesions is apraxia. This deficit is neither sensory, because subjects still have normal visual and other sensory functions, nor motor, because the patients are not paralyzed. However, they seem unable to form the "plan" or "idea" for a movement. Thus, this deficit is interposed between sensation and action and appears to result from a disruption in the early stages of movement planning (Critchley, 1953, for review). In recent years, several studies in humans and monkeys point to a newly appreciated role of the PPC in programming actions, and more specifically, in transforming sensory signals into plans for motor behaviors (Mountcastle et al., 1975; Gnadt and Andersen, 1988; Goodale and Milner, 1992; Rizzolatti, Riggio, and Sheliga, 1994; Andersen, 1995; Mazzoni et al., 1996b; Sakata et al., 1997; Snyder, Batista, and Andersen, 1997).

A new and emerging view of the PPC is that it contains an anatomic map of intentions (Andersen et al., 1997; Snyder, Batista, and Andersen, 1997) (figure 36.1). Included in this map for movement planning is area LIP, which appears to be specialized for making saccades. A region medial and posterior to area LIP, PRR, is specialized for planning reach movements. This area likely includes the dorsal aspect of the parieto-occipital (PO) area and the medial intraparietal (MIP) area. A third task-specific area is the anterior intraparietal (AIP) area, located just rostral to area LIP, which appears to be specialized for grasping (Sakata et al., 1997). Finally, within the fundus of the intraparietal sulcus is an area with somatosensory receptive fields around the mouth and head and visual receptive fields that in many cases prefer stimuli moving toward the animal's mouth and head (Duhamel, Colby, and Goldberg, 1998). This ventral intraparietal (VIP) area may be specialized for "grasping" with the mouth.

In this review, we cover studies revealing the role of PPC in intention. Also of interest are studies examining the coordinate frame in which space is represented in area LIP and PRR. This work was designed to determine how different modalities that are represented originally in different coordinate frames are brought together in the PPC. We also discuss how communication may be achieved between these different areas, which are highly interconnected anatomically (Andersen et al., 1990; Blatt, Andersen, and Stoner, 1990), and how these areas might incorporate common processing strategies for the orchestration of complex behaviors requiring hand–eye coordination. As we will see, area LIP and PRR appear to use a common mechanism for representing visually and auditorily cued spatial locations. The resulting representation has the computationally powerful

R. A. ANDERSEN, A. P. BATISTA, L. H. SNYDER, C. A. BUNEO, and Y. E. COHEN   Division of Biology, California Institute of Technology, Pasadena, Calif.

Anatomical Organization for Actions in the Posterior Parietal Cortex
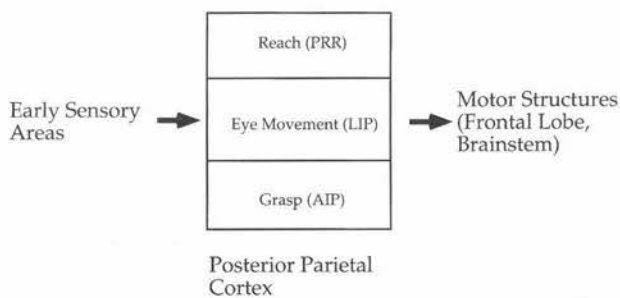

FIGURE 36.1 The posterior parietal cortex contains separate areas specialized for reach movements (area PRR), saccades (area LIP), and grasping (area AIP).

feature that it is distributed and can be read out by other areas of the brain as several different coordinate frames, for example, eye-, head-, body-, or even world-centered. Finally, we review research that finds that the representations of space in both area LIP and PRR are updated across eye movements for the remembered locations of targets for movement.

Intentions to saccade and reach

There is a considerable amount of suggestive evidence that the PPC has an intentional role, but it has been very difficult to design experiments that dissociate intention-related activity from activity related to attention. This difficulty arises from the fact that monkeys (and humans) attend to locations where they plan to make movements. In a recent study, we designed a task specifically to isolate intention-related activity (Snyder, Batista, and Andersen, 1997). We reasoned that activity in the PPC should be indifferent to the type of movement planned by the animal if it is only related to attention. Thus, if the monkey planned a reach or a saccade to the stimulus at the same location, there should be little or no difference in activity if it is primarily dependent on attention. However, if the activity depends strongly on the movement the monkey plans, then this activity would be related to the animal's intention.

Animals were trained to memorize the location of briefly flashed visual stimuli in an otherwise dark room and to plan either an eye or an arm movement to the cued location, the type of movement being instructed by the color of the flashed stimulus. Figure 36.2 demonstrates our typical result—that the activity in the memory period depended largely on the type of movement the animal planned. Approximately two thirds of PPC neurons showed a significant response in the memory pe-

riod for only one of the two movement plans. The remaining one third of the cells responded to both plans. However, approximately one half of the cells responding for both movements appeared to be forming a default plan for a particular type of movement, as shown in an additional control and thus also were intention related. We proposed that these cells were coding "covert" plans for movement. An example of one of these covert planning cells is shown in figure 36.3. This cell had activity during the memory period regardless of whether the animal planned a reach or a saccade into its receptive field. In the control experiment, we had the animal perform a two-movement task, in which he planned and
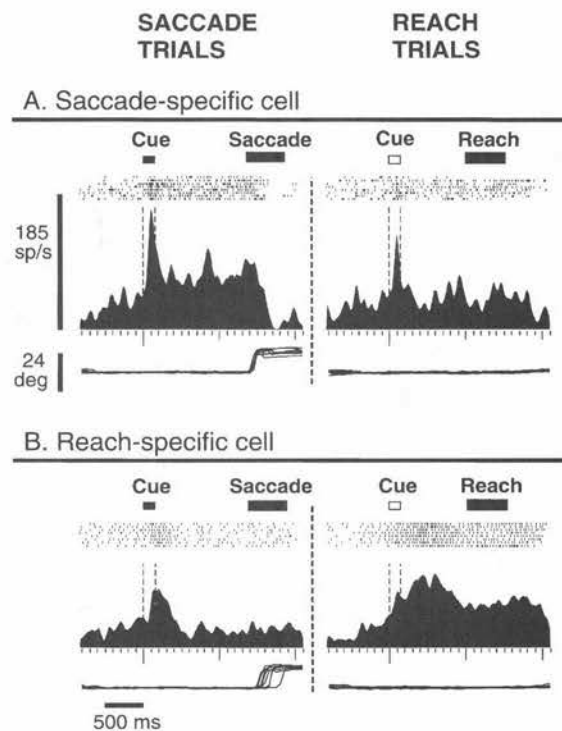

FIGURE 36.2 Responses of two intention-specific neurons in the delayed-saccade (left) and delayed-reach (right) tasks. Each panel shows timing of peripheral flash (Cue: red flashes indicated by filled bars, green flashes by open bars) and response (Saccade or Reach); eight rows of rasters corresponding to every third action potential recorded during each of eight trials; a spike density histogram of neuronal activity, generated by convolution with a triangular kernel aligned on cue presentation, with cue onset and offset indicated by dashed lines; and eight overlaid traces showing vertical eye position. Neuronal responses in the cue interval (50 ms before to 150 ms after cue offset) were nonspecific. However, during the delay interval (150–600 ms), firing depended specifically on motor intent. (A) A cell showing elevated delay period firing before a saccade (left) but not before a reach (right). For illustration purposes, data for this cell were collected using a fixed delay interval. (B) A second cell showing reach rather than saccade specificity during the delay interval. (Reprinted from Snyder, Batista, and Andersen, 1997.)

	Preferred Direction	Null Direction

SACCADE TASK Cue / Cue

40 sp/s

REACH TASK

500 ms

DISSOCIATION TASK

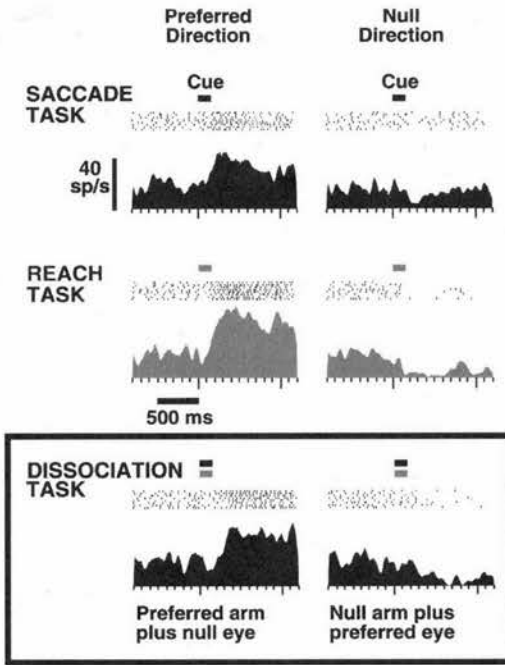Preferred arm plus null eye / Null arm plus preferred eye

FIGURE 36.3 An intention-specific neuron whose motor specificity was revealed by the dissociation task. Delay activity was greater before movements toward the receptive field (Preferred Direction) compared with away (Null Direction) in both delayed saccade (top row) and reach (middle row) tasks. Thus, in single-movement tasks, the neuron appears to code remembered target location independent of motor intent. However, motor specificity was revealed in the dissociation task (bottom row). Firing was vigorous before a preferred reach combined with a null saccade (bottom left) but nearly absent before a preferred saccade plus null reach (bottom right). Thus, when both a reach and a saccade were planned, delay activity reflected the intended reach and not the intended saccade. Panel formats are similar to figure 36.1. Every other action potential is indicated by one raster mark. (Reprinted from Snyder, Batista, and Andersen, 1997.)

made eye and reach movements simultaneously in opposite directions. The bottom panels of figure 36.3 illustrate that when the animal planned an arm movement into the receptive field but an eye movement outside the receptive field, the cell was active, but when it planned the eye movement into the receptive field and the arm movement outside of the receptive field, the cell was not active. Thus, it would appear that the animal was making a "default" plan to reach that was not executed. Because half of the cells responding to both plans demonstrated a covert preference for either saccades or reaches, overall 84% of the PPC cells tested had activity during the memory period specifying the intent of the animal.

The intended movement activity was anatomically segregated depending on whether it was related to plans for saccades or reach. Perhaps not surprisingly, eye movement planning activity was found predominantly in area LIP. This finding is very consistent with previous research, which has indicated that area LIP can be considered the "posterior eye field" for the processing of saccadic eye movements (Andersen, Brotchie, and Mazzoni, 1992). Area LIP cells have presaccadic bursts of activity (Barash et al., 1991); saccade deficits result after lesions in area LIP (Lynch and McLaren, 1989; Li, Mazzoni, and Andersen, 1999); there are strong anatomic projections from area LIP to other saccade centers, such as the superior colliculus, frontal eye field, and dorsallateral pons (Lynch, Graybiel, and Lobeck, 1985; Asanuma, Andersen, and Cowan, 1985; Blatt, Andersen, and Stoner, 1990; Andersen et al., 1990); and electrical microstimulation of area LIP evokes saccades without other body movements (Thier and Andersen, 1996, 1998). The reach selective responses were found medial and posterior to area LIP, in a band of cortex that likely includes areas MIP to PO. We referred to this functionally defined region of the PPC as the parietal reach region (PRR).

The focus of attention and the planning of eye movements are linked tightly, so it could be argued that the selectivity in area LIP is due to the fact that animals attend to where they plan to saccade but not to where they plan to reach, and the differential activity reflects this difference in attention (Colby and Goldberg, 1999). However, this line of reasoning would require PRR neurons also to be most active when eye movements are planned in their receptive fields; instead, we see the reverse phenomena, with activity being greatest when reaches are planned into their receptive fields. Moreover, in the following experiments, attention was maintained the same and the animals were asked to change their movement plans. As we see, when attention is identical across trials, the activity of PPC neurons changes dramatically depending on the animals' plans.

Changing movement plans without changing the locus of attention

A direct prediction from the aforementioned conclusions is that activity should shift between areas LIP and PRR when monkeys change their movement plans. We have tested this prediction with the paradigm shown in figure 36.4 (Snyder, Batista, and Andersen, 1998). The experiment began in a similar manner to the aforementioned one, with a flash of light instructing a particular type of movement to the location of the flash inside the receptive field of a cell. However, in the later period of some of the trials, this plan either was changed by a second flash of a different color or was reaffirmed by a flash of the same color. The animals did not know what the subsequent flash
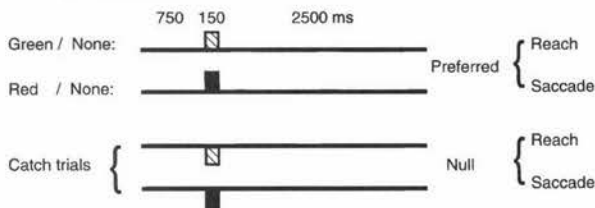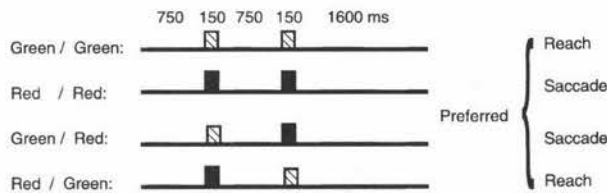
FIGURE 36.4 Time course of eight single- and double-flash trials. The experiment was designed to force the animal to attend to the spatial location and color of both flashes. A 150-ms flash appeared 750 ms after fixation began. Red and green flashes instructed saccades and reaches, respectively. On half of the trials, a second flash occurred 750 ms later at the same location as the first, sometimes instructing a change in the motor plan but never shifting spatial attention. Fixation light offset, 2.5 s after the first flash, signaled the animal to perform the most recently instructed movement. For one animal, double-flash trials also occurred for the null direction (not shown). (Reprinted from Snyder, Batista, and Andersen, 1998.)
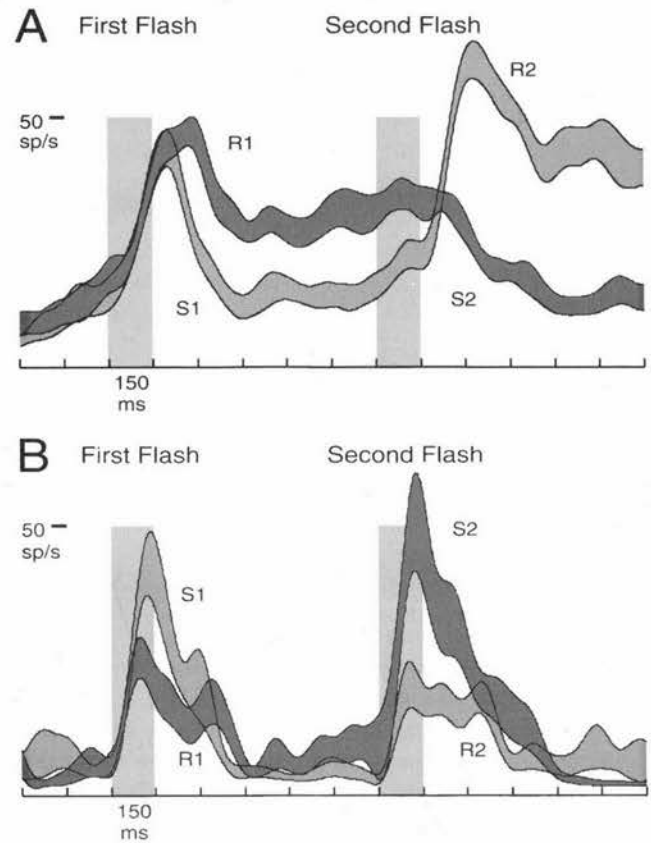
FIGURE 36.5 (A) Intention-selective responses of a parietal reach region (PRR) neuron to changes in motor plan, from a saccade to a reach (light trace) or from a reach to a saccade (dark trace). Sustained activity resulting from an instruction to plan a reach (R1) was abolished when a second flash changed 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). The 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 (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 to 12 trials ±1 standard error of the mean (SE). Shading indicates the time of one 150-ms flash. Data were smoothed before plotting (121-point digital low-pass filter, transition band 20–32 Hz). (Reprinted from Snyder, Batista, and Andersen, 1998.)

would instruct, and because these second flashes always appeared at the same location as the first flashes, the monkeys' attention was the same whether the plan was changed or reaffirmed.

The response was related strongly to the animals' intentions. Figure 36.5 shows the activity of a reach neuron (figure 36.5A) and a saccade neuron (figure 36.5B) when the monkey changes plans from a reach to a saccade and vice versa. The activity of the neurons is much stronger when the preferred movement is cued. In the reach cell illustrated in figure 36.5A, the activity also is much higher during the first and second delays when the monkey is planning a reach instead of a saccade. These dramatic plan-related changes in neural response during the delay are taking place without the animal emitting any behavior at all. The animal is simply changing his intentions during the delay period.

The plan dependency across the population of PRR cells can be seen in figure 36.6A. The response to the first flash is larger when it is green and therefore is instructing a reach. This reach-planning activity remains high during the first delay period. The middle panel shows the responses to a second, green flash instructing a reach, segregated into two plots, depending on whether this second flash reaffirmed or changed the

plan. In this instance, the response to the identical green flash, under identical attention conditions, was much stronger if the animals were required to change their plans. Thus, it can be concluded that a large com-

ponent of the flash-triggered activity actually reflects a shift in plans. The plots on the right show that this change-in-plan–specific activity is not a result of the novelty. These plots show the responses to the second flash when it is red and instructing an eye movement. These responses were small for the nonpreferred plan, regardless of whether it was a change or reaffirmation of the previous plan. Thus, the enhanced response to the flashes was present only when there was a change of plan to the preferred plan. The same result was found for LIP neurons, but saccades were the preferred plan.

Coding the next planned movement in the lateral intraparietal area and the parietal reach region

Using a memory double saccade paradigm, we found that most of area LIP neurons code the next planned eye movement (Mazzoni et al., 1996b). As shown in figure 36.7D, for a representative neuron, when the second target of the planned sequence of movements fell within the receptive field of the LIP cell but the animal was planning the first eye movement outside of the receptive field, this cell showed only a brief response to the stimulus and was not active in the memory period. However, if the same target fell within the receptive field of the cell and it was the target for the first eye movement, then the cell was active during the memory period (figure 36.7C). This result is typical of most (77%) LIP neurons. There also was a minority of cells with activity for the second target during the memory phase, and these cells appear to hold the memory of the location of the second target.

We recently performed a similar double-movement experiment in the PRR but required the monkey to plan two reaches instead of two saccades (Batista et al., 1998). In this task, we first cued the monkey to a location for a reach within the receptive field of the neuron. However, during the delay period, if we flashed a second target outside the receptive field of the cell, the animal was required to make the reach first to that target. At the end of the delay, the animal reached to this second target and another delay period began in which he then planned a movement to the first flashed target location. At the end of this second delay, the animal made a second limb movement to the remembered location of the first target. We found that, similar to LIP cells, PRR cells ceased firing to the remembered location of the first reach target when the monkey was planning an arm movement to the location of the second target, outside the receptive field of the cell. Moreover, we found when we reversed the sequence of targets so that the second target and first reach were in the receptive field, the activity still was always only present when the next

planned movement was into the receptive field. Thus, PRR shares another similarity with area LIP, with PRR neurons coding the next planned movement in double-movement tasks. This result adds further support for the idea that a large component of both PRR and LIP activity reflects the animals' plans or intentions for movement.

The coordinate frame of the lateral intraparietal area for visual stimuli

Lateral intraparietal neurons have receptive fields much like neurons in other visual areas, which are in the coordinates of the retina or eye—that is, the locations in space that activate these cells move with the eyes. However, we also have found that the activity of these cells is modulated by eye position and head position (Andersen et al., 1990; Brotchie et al., 1995; Snyder, Grieve, et al., 1998). Neural network simulations show that these "gain field" effects can serve as the basis for a distributed coding in other coordinate frames besides an eye-centered frame (Zipser and Andersen, 1988). Thus, for instance, neurons in another part of the brain that receive inputs from area LIP could construct receptive fields in head-centered coordinates by exploiting the eye position gain fields. Likewise, the combination of eye and head position gains can be used to construct body-centered representations (figures 36.8 and 36.9).

Coordinate frame for the lateral intraparietal area for auditory stimuli

Area LIP is considered an extrastriate visual area. It is at approximately the same level as area V4 (Andersen et al., 1990; Blatt, Andersen, and Stoner, 1990) when considered within the hierarchy of visual areas based on feedforward and feedback patterns of corticocortical connections (Maunsell and van Essen, 1983). Thus, it is imbedded deeply in the extrastriate visual cortex and occupies a position relatively early (i.e., close to V1) in the visual pathway. This is reflected in the brisk responses of area LIP to visual stimuli, even when the animal is ignoring the stimulus (Linden, Grunewald, and Andersen, 1997) or is anesthetized (Blatt, Andersen, and Stoner, 1990).

LIP neurons usually do not respond to auditory stimuli. However, because area LIP plays a major role in processing saccades and because monkeys obviously can make saccades to auditory stimuli, we hypothesized that LIP neurons would be active when the monkey used auditory stimuli for the purpose of making eye movements. This is in fact the case (Mazzoni et al.,
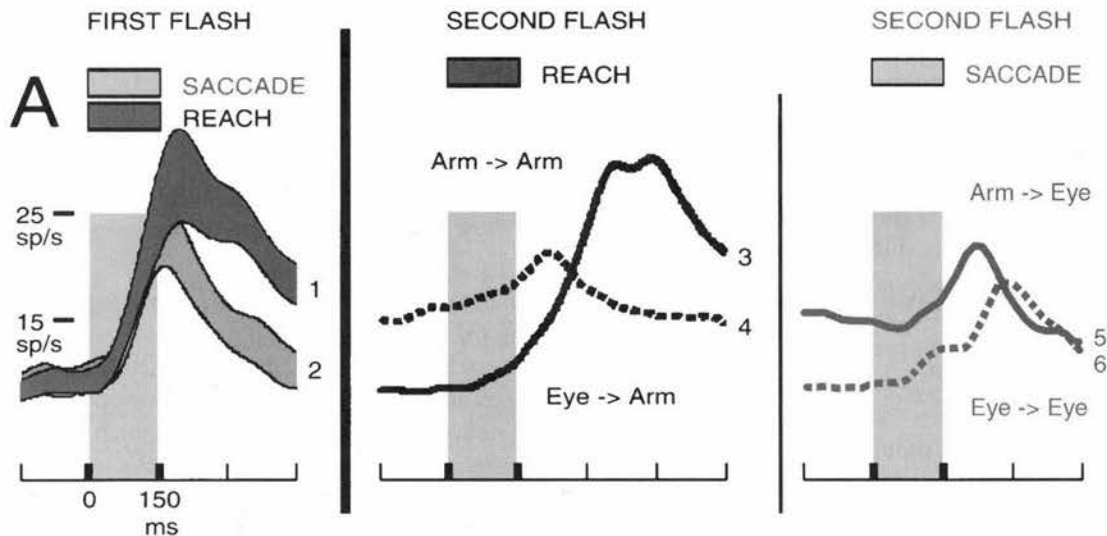
FIGURE 36.6 Population data from the parietal reach region (PRR) ([A] average of 17 cells). Responses to the first (left panel) and second (right and middle panels) flashes, instructing either a saccade (light) or a reach (dark) are shown. Second flashes could instruct a preferred (middle) or nonpreferred (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 first flash (1). For nonpreferred movements, countermanding and affirming flashes elicited similar comparatively small responses (5 vs. 6). Format as in figure 36.5, except that SE was calculated across cells rather than across trials (left). (Reprinted from Snyder, Batista, and Andersen, 1998.)

1996a; Grunewald, Linden, and Andersen, 1997). We also have determined the reference frame of these auditory triggered responses in a memory-guided eye movement task. In very early levels of the brain dedicated to determining the spatial location of auditory stimuli, cells have auditory receptive fields in head-centered coordinates. These head-centered fields are constructed using interaural time, intensity, and spectral cues. Conversely, in area LIP, we found only 33% of the cells had fields in head-centered coordinates whereas a surprising 44% had fields that were in eye-centered coordinates (Stricanne, Andersen, and Mazzoni, 1996). The remaining 23% of the cells had fields that were intermediate between these two coordinate frames. One parsimonious interpretation of these results is that area LIP is responsible for converting head-centered auditory signals into eye-centered coordinates. The neurons with auditory responses in area LIP typically also have eye position gain fields. These gain effects could provide the mechanism for converting auditory signals from a head-centered to an eye-centered representation.

These findings have two important implications. First, the fact that area LIP only responds to auditory stimuli when they are of oculomotor significance to the animal presents a very different view of multimodal integration than is commonly held. It suggests that area LIP usually is a default visual area, involved in transforming visual stimuli into eye movement plans. How-

ever, when auditory stimuli are deemed to be targets for saccades, then LIP becomes active. Second, when auditory signals are relayed to area LIP, they are transformed into the eye-centered reference frame of this area. This result suggests that vision provides the basic map for spatial location within area LIP. As we will see, these two ideas also can be extended to PRR. In fact, for many forms of extrapersonal spatial analysis and behavior, space may be represented in eye coordinates and other modalities may be brought into the eye-centered representation when multimodal integration is required. This idea certainly makes good ecological sense for vision and audition because audition can give us the general location of a stimulus but only our high-resolution vision can locate precisely a target of interest. This concept may explain the ventriloquist effect, in which visual stimuli tend to dictate the perceived spatial location of the auditory stimuli. In this illusion, if we see someone's lips moving but the speech source is from a different location in space, we nonetheless perceive the sound as coming from the moving lips.

Reference frame for the parietal reach region

We recently examined the reference frame for reach-planning activity in PRR. One possibility is that the reach activity is in the coordinates of the limb, coding the motor error for a limb movement. Alternatively,
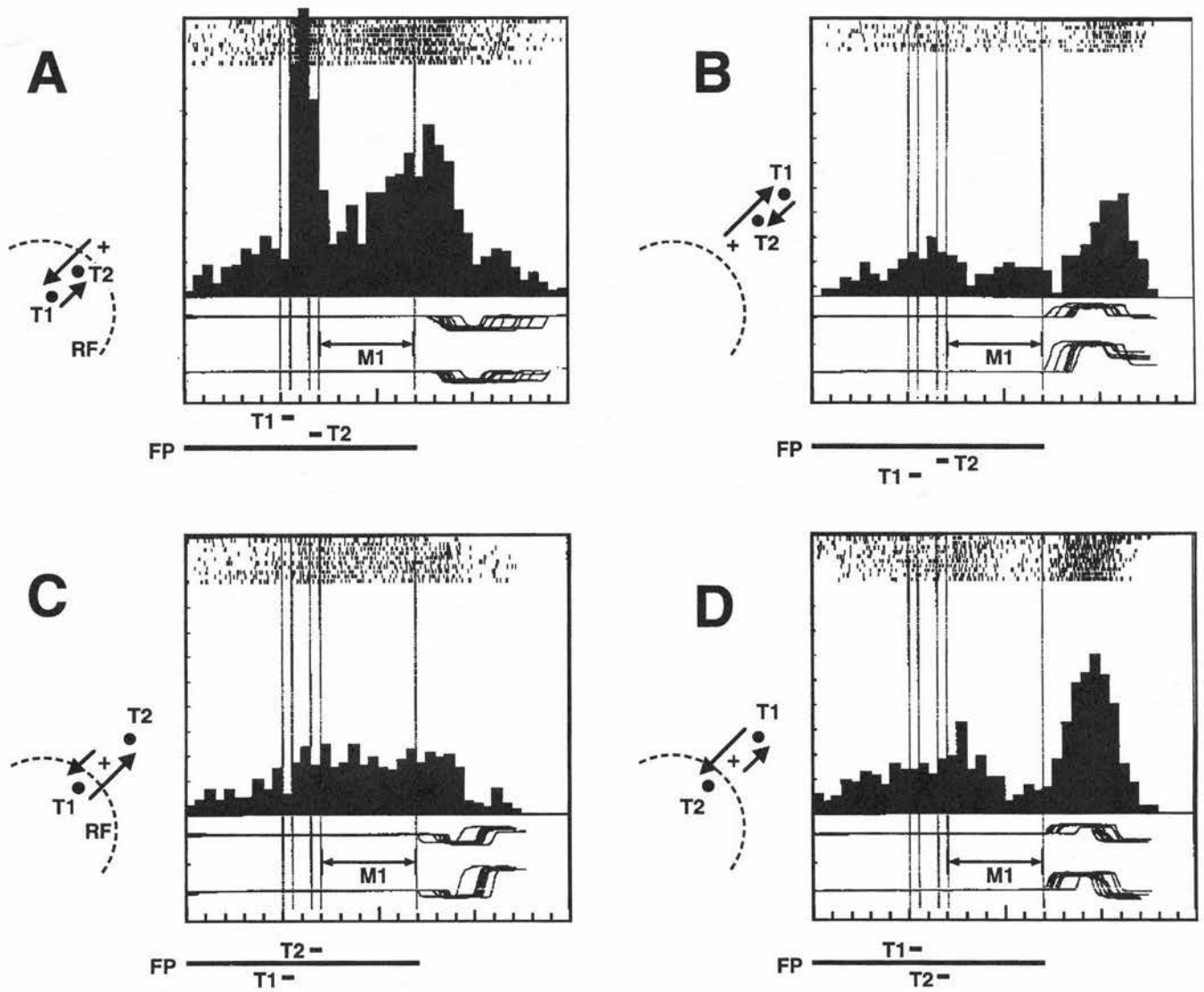
FIGURE 36.7   Activity of a lateral intraparietal (LIP) neuron in four different sequences of a double-saccade paradigm. Each panel has a plot that includes, from top to bottom, the spike rasters for each trial, the time histogram (binwidth, 50 ms) of the firing rate (20 Hz/division in A–C, 25 Hz/division in D), and the horizontal and vertical eye positions (25 degrees/division; abscissa: 100 ms/division). Vertical dotted lines and the thick horizontal lines below each panel again show the onset and offset of the visual stimuli. Diagrams to the left of each panel show the spatial arrangement of the first and second target (T1 and T2, respectively), the first and second saccades (arrows), and the neuron's receptive field (RF). (Reprinted from Mazzoni and associates, 1996b.)

PRR activity could be referenced to the eye, similar to activity in area LIP. We differentiated between these two possibilities by having monkeys make the same reach, but with the eyes gazing in different directions, or alternatively having them reach to the same location with respect to the eyes, but with the limbs starting from different initial positions. If the neurons were coding in eye coordinates, we would expect different activities for the former condition because identical reaches are made to different retinal locations. However, if the cells are coding in limb coordinates, then activity should vary in the latter condition because limb movements in different directions are made to the same location with respect to the retina. We found that most PRR cells code reaches in eye coordinates (Batista et al., 1998). The eye-centered responses often were modulated by eye position (Batista et al., 1998). Thus, PRR appears to have the same distributed representation of space as LIP, with their neurons having eye-centered receptive fields modulated by gain fields for eye and other body part positions (figure 36.8).

Establishing a common coordinate frame for both LIP and PRR led us to a rather nonintuitive prediction–that reaches to the remembered locations of sounds in the

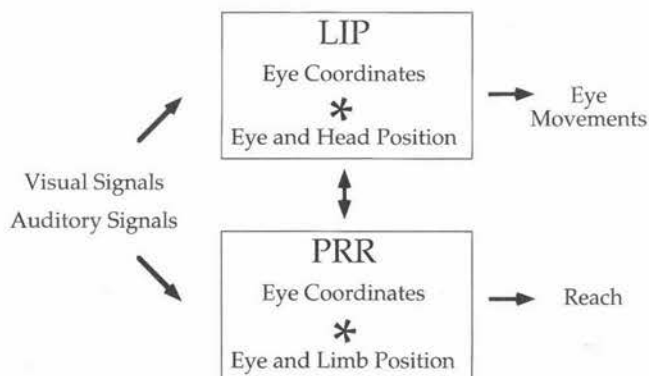## PRR and LIP Share a Common Coordinate Frame

FIGURE 36.8   Both visually and auditorily cued locations are represented in eye coordinates in the lateral intraparietal (LIP) area and the parietal reach region (PRR). Also, both areas have gain modulation of the eye-centered receptive fields by eye and body part positions.

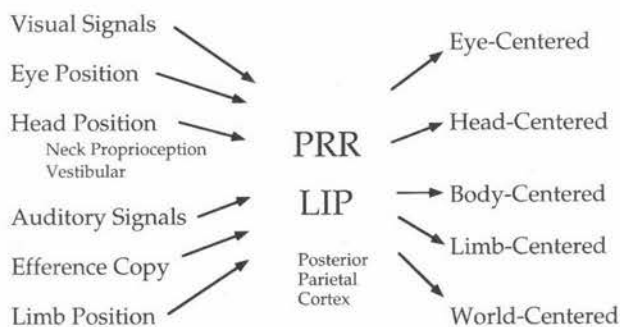## A Distributed Code for the Representation of Space

FIGURE 36.9   The eye-centered visual and auditory receptive fields of the parietal reach region (PRR) and the lateral intraparietal (LIP) area are modulated by signals specifying eye, head, and limb position. These modulations produce a common, distributed representation in both areas that can be read out by other parts of the brain in a variety of coordinate frames (including eye, head, body, and even world centered), depending on how the population of neurons in area LIP and PRR are sampled.

dark should be coded in eye-centered coordinates. Of course, in principle, there is no need for this sort of representation. Head-centered auditory signals could be converted directly to limb coordinates for making reaches; there is no need to have an intermediate step of converting these reach signals to eye coordinates. However, if there is a common coordinate frame for both PRR and LIP, then the reach activity should code the target location in eye-centered coordinates and be modulated by eye and limb position signals. Furthermore,

the results from the auditory saccade experiments in area LIP, outlined previously, also predict that the auditory signals would be transformed into eye-centered receptive fields in PRR. This prediction has been substantiated in recent experiments from our laboratory (Cohen and Andersen, 1998). We find that reaches to auditory targets often are coded in eye coordinates in PRR, and these eye-centered receptive fields are strongly gain-modulated by both eye and limb positions. Thus, auditory and visual signals are represented in a similar distributed manner in both LIP and PRR, with eye-centered receptive fields modulated by eye and body position signals (figure 36.8). The advantage of a shared reference frame may be to coordinate communication between the two areas, for instance, during tasks that require the close coordination of the eyes and hands.

Updating lateral intraparietal and parietal reach region spatial representations across saccades

To make an eye movement to a remembered location after intervening saccades requires a mechanism for updating the location of the target. Sparks and Mays (1980) first addressed this intriguing problem in physiologic experiments in the superior colliculus. They found that cells in the intermediate layers updated the location of the next planned eye movement in eye-centered coordinates across saccades. We later showed a similar updating in LIP (Gnadt and Andersen, 1988). Duhamel and

The Remembered Locations Are Maintained in Eye Coordinates Across Saccades in Both PPR and LIP
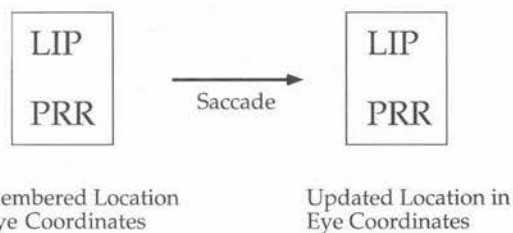

FIGURE 36.10   Remembered locations are updated in eye coordinates in both the lateral intraparietal (LIP) area and the parietal reach region (PRR). This updating is required not only to ensure that eye-centered locations remain invariant across eye movements, but also for other coordinate frames as well. For instance, when the eye position changes, the eye-gain fields change, and if the eye-centered locations of remembered stimuli are not updated, the correct head-centered location cannot be read out from the population of LIP or PRR neurons.

associates (1992) extended these results to show that a second eye movement was not necessary for this updating to take place. Although they interpreted this updated activity to be sensory, the results of Snyder, Batista, and Andersen (1997, 1998) suggest that this activity may in fact represent default plans for eye movements to the flashed second targets.

We recently asked whether this same updating process takes place in PRR. We presented a visual target for a reach that a monkey was required to remember. However, during the memory period, we then had the monkey make a saccade to fixate a new location in space. Routinely, the remembered location of the reach target was updated in eye coordinates to take into account the change in eye position (Batista et al., 1998). For example, if the monkey made a saccade that brought the remembered location of the target into the retinal receptive field of the PRR neuron, then it became active during the delay period before the reach. If the saccade brought the remembered location out of the receptive field of PRR cell, then it fell silent. Again, LIP and PRR were found to share an important similarity, both updating remembered locations in eye coordinates across saccades (figure 36.10). We also have seen the same updating in eye coordinates for locations cued by auditory targets (Cohen and Andersen, 1998).

This finding has important consequences for reading out the distributed representation of space accurately in nonretinal coordinates. If the eyes move, the eye position signals and gain modulations in LIP and PRR change in accordance with the new eye position. If the remembered retinal location of a target remains the same after the eye movement it is coded incorrectly in head- or body-centered coordinates. Thus, the updating of location in eye coordinates is necessary to read out the correct location with respect to the head or body.

Conclusions

The results reviewed previously show that areas LIP and PRR share several common features, even though one area is related to planning eye movements and the other is related to activity in reach movements. These common features include the following:

1. Both code visual and auditory targets in eye centered coordinates (figure 36.8);

2. Both demonstrate gain fields for eye and other body part positions (figure 36.9);

3. Activity in both areas code the next planned movement; and

4. Planned movement activity is updated across eye movements (figure 36.10).

These common features, particularly points 1 and 2, indicate that the two areas use a common coordinate frame. This coordinate frame is distributed and can be read out by other areas in several different reference frames. The specificity of their activity for the type of movement, and the fact that the cells only code the next planned movement (point 3), indicates that both areas code intentions to move. Whether these two areas of the PPC establish the basic rules for processing for other areas in the PPC remains to be seen.

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