

29 Multisensory Representations of Space in the Posterior Parietal Cortex

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Introduction

Actions are often directed toward the location of sensory stimuli. It can be argued that a large component of our mental repertoire is dedicated toward directing motor effectors toward the location of a sensory stimulus (Snyder, 2000). The diverse computations underlying this capacity are often grouped under the rubric of the sensorimotor transformation.

In this chapter, we focus on the importance of one component of the sensorimotor transformation, reference-frame (coordinate) transformations. Reference-frame transformations are not trivial, because the location of a sensory stimulus is often coded in a reference frame that is different from the one used by the eventual motor effector. In particular, we examine the role of the posterior parietal cortex (PPC) in reference-frame transformations. We introduce evidence that an aspect of the reference-frame transformation is to represent target locations in a common reference frame in a significant population of neurons in two areas of the PPC. This common reference frame is an eye-centered representation that is “gain” modulated by such factors as eye, head, body, or initial hand position. The advantage of this representation is that it allows the PPC to maintain representations of many different reference frames that can be read out depending on the cognitive and computational needs of the ongoing task. In the next section we introduce the concept of a reference frame and reference-frame transformations, and then discuss the role of the PPC in movement planning and reference-frame transformations.

Reference frames and reference-frame transformations

A reference frame can be defined as a set of axes that describes the location of an object. Many different reference frames can be used to describe the location of

the same object. For instance, imagine that you are sitting in the park and looking at a flower in a field. The location of the flower can be described based on the pattern of light that falls on your eyes and retinas. The location of the flower can also be described relative to your head or body position. It is also possible to describe the flower’s location in an extrinsic reference frame, one that is based on objects in the world. For example, the flower’s location can be described relative to its position in the field or the location of the bench on which you are sitting.

Describing the location of an object in different frames of reference is not simply an academic exercise. Instead, it is a critical computation that underlies our capacity to engage in different types of goal-directed behaviors (Andersen, Snyder, Bradley, & Xing, 1997; Colby, 1998; Graziano, 2001; Pouget & Snyder, 2000). For instance, if you want to look at the flower, it is important to know the location of the flower relative to your eyes and head. In contrast, if you want to pick the flower, it is important to be able to compute the location of the flower relative to your arm and hand.

Although we have focused our description of reference frames on visual stimuli, we can also describe the location of other modality stimuli. However, the computations underlying this capacity initially depend on modality-specific mechanisms. Describing the location of a visual stimulus depends initially on the pattern of light that falls on the retinas and the resulting activation of photoreceptors. In contrast, describing the location of an auditory stimulus depends initially on the brain’s capacity to compute interaural level and timing differences and monaural spectral cues (Blauert, 1997; Cohen & Knudsen, 1999; Middlebrooks & Green, 1991). Locating a tactile stimulus uses a third mechanism that is based on the pattern of activity in the array of tactile receptors that lie beneath the skin’s surface. This mechanism is akin to that used by the visual system in that both code the location of

a stimulus based on the activity in a topographic array of receptors.

The motor system also codes the movement of effectors in particular reference frames (Klier, Wang, & Crawford, 2001; Soechting & Flanders, 1995; Sparks, 1989; Sparks & Mays, 1990). Arm movements are coded based on the difference between initial and final hand position (a limb-centered reference frame; Soechting & Flanders, 1992, 1995). Similarly, eye movements are coded based on the difference between current and desired eye position (an eye-centered reference frame; Sparks, 1989; Sparks & Mays, 1990).

Given these descriptions of motor and sensory reference frames, a computational issue becomes immediately evident. Namely, how can sensory information that is collected in one reference frame guide motor acts that are calculated in a different reference frame? For instance, how can an arm movement that is calculated in a limb-centered reference frame be directed toward a sound whose location is calculated in a head-centered reference frame? The solution to this reference-frame problem is to transform the representation of a sensory stimulus into one that is appropriate for the eventual motor act (Flanders, Tillery, & Soechting, 1992; Ghilardi, Gordon, & Ghez, 1995; Kalaska & Crammond, 1992; Soechting & Flanders, 1989a, 1989b). The PPC plays an important role in this reference-frame transformation. In the next section we highlight the role of the PPC in movement planning and present evidence that, as one element of this reference-frame transformation, the PPC represents target locations that are used in movement planning in a common reference frame.

Role of the PPC in movement planning

A large component of PPC activity appears to be dedicated to the coordination of different movement plans. Although we will stress here the role of the PPC in movement planning, neurons in areas of the PPC are modulated by other cognitive intermediates of sensorimotor transformation. An analysis of these different signals is outside the scope of this discussion but can be found elsewhere (see, e.g., Andersen & Buneo, 2002; Colby & Goldberg, 1999; Kusunoki, Gottlieb, & Goldberg, 2000).

Three functionally distinct movement-planning regions have been identified so far: the lateral intraparietal area (area LIP), the parietal reach region (PRR), and the anterior intraparietal area (area AIP). LIP neurons are modulated preferentially by sensory targets that indicate the future location of an eye movement (Platt & Glimcher, 1997; Snyder, Batista, & Andersen,

1997, 1998, 2000). The PRR, which overlaps with the medial intraparietal area and parieto-occipital cortex, codes reaches (Battaglia-Mayer et al., 2000; Calton, Dickinson, & Snyder, 2002; Colby & Duhamel, 1991; Eskandar & Assad, 1999; Galletti, Battaglini, & Fattori, 1993, 1995; Galletti et al., 1996, 1997, 1999, 2001; Johnson, Ferraina, Bianchi, & Caminiti, 1996; Snyder, Batista, et al., 1997, 1998, 2000). AIP neurons are modulated preferentially by the size, shape, and orientation of objects that specify a particular grasp (Gallese, Murata, Kaseda, Niki, & Sakata, 1994; Murata, Gallese, Kaseda, & Sakata, 1996; Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Sakata, Taira, Kusunoki, Murata, & Tanaka, 1997).

The different roles of area LIP and PRR in movement planning have been demonstrated in delayed eye-movement and delayed reach tasks in monkeys (Snyder et al., 1997). In the delayed eye-movement task, monkeys made saccades (rapid eye movements) to the location of remembered visual targets. In the delayed reach task, monkeys made reaches to the location of remembered visual targets. Data were analyzed during the period that followed visual-target offset but before any movements were made to the remembered targets. Delay-period activity was examined, because it is not confounded by the presence of the visual stimulus or by the movement itself (Gnadt & Andersen, 1988).

An analysis of the neural activity during this delay period indicated that LIP neurons responded significantly more during the delayed eye-movement task than during the delayed reach task. The response pattern of PRR neurons was the opposite: PRR neurons responded significantly more during the delayed reach task than during the delayed eye-movement task. These two results are consistent with the hypothesis that LIP neurons are preferentially involved in coordinating eye-movement plans, whereas PRR neurons are preferentially involved in coordinating reach plans.

The third identified movement planning area, area AIP, appears to be specialized for grasp planning (Sakata et al., 1997). Reversible inactivations of area AIP produce deficits in a monkey's ability to make the precise finger movements that are required to shape his hand to appropriately grasp an object (Gallese et al., 1994). Supporting this behavioral finding, a neurophysiological study demonstrated that AIP neurons respond preferentially to (1) specifically shaped and oriented objects and (2) the specific hand configurations that are required to properly grasp an object (Murata et al., 1996). These behavioral and neurophysiological studies, as well as other studies (Murata et al., 2000; Nakamura et al., 2001; Sakata, Taira, Murata, & Mine, 1995; Sakata et al., 1999), are consistent with the

hypothesis that area AIP plays a role in the coordination of grasp plans.

This parceling of the PPC into functionally distinct regions is not limited to non-human primates. Functional-imaging and patient studies indicate a similar organizational schema for the human PPC (Binkofski et al., 1998; Connolly, Goodale, DeSouza, Menon, & Vilis, 2000; DeSouza et al., 2000; Jancke, Kleinschmidt, Mirzazade, Shah, & Freund, 2001; Karnath, Ferber, & Himmelback, 2001; Kawashima et al., 1996; Luna et al., 1998; Rushworth, Paus, & Sipila, 2001). These studies have identified functional regions in the human PPC that are specialized for eye movements, reaches, and grasps.

Insofar as regions of the PPC are involved in movement planning, it is reasonable to predict that PPC neurons are involved in the coordination of movement plans to targets of different sensory modalities, and this proposition has been borne out in several recent experiments. LIP and PRR neurons respond to auditory and visual stimuli that indicate the future location of a movement (Cohen & Andersen, 2000; Cohen, Batista, & Andersen, 2002; Grunewald, Linden, & Andersen, 1999; Linden, Grunewald, & Andersen, 1999; Mazzoni, Bracewell, Barash, & Andersen, 1996; Stricanne, Andersen, & Mazzoni, 1996). Figure 29.1A shows a PRR response profile that was generated while a monkey made reaches to the remembered location of auditory stimuli. Figure 29.1B shows the response profile from a different PRR neuron that was generated while a monkey made reaches to the remembered location of visual stimuli. All aspects of the task modulated both neurons, since they responded during the presentation of the sensory target, during a delay period that followed the offset of the sensory cue, and during the reach period itself. Functional imaging studies in humans also suggest that the PPC contributes to tasks that use auditory and visual stimuli (Bremmer et al., 2001; Bushara et al., 1999; Griffiths et al., 1998).

Although PPC neurons respond to both auditory and visual targets, they do not appear to code these sensory modalities in a completely similar manner. For example, auditory responses in area LIP appear to be the result of behavioral training in which a monkey has been trained to associate the auditory stimulus with a future eye movement (Grunewald et al., 1999; Linden et al., 1999). In contrast, in untrained or even anesthetized animals, LIP neurons respond robustly to visual stimuli (Grunewald et al., 1999; Blatt, Andersen, & Stoner, 1990). Another difference is that the spatial selectivity of PPC neurons for auditory-target and visual-target locations is different (Cohen et al., 2002; Grunewald et al., 1999; Linden et al., 1999). This difference can be

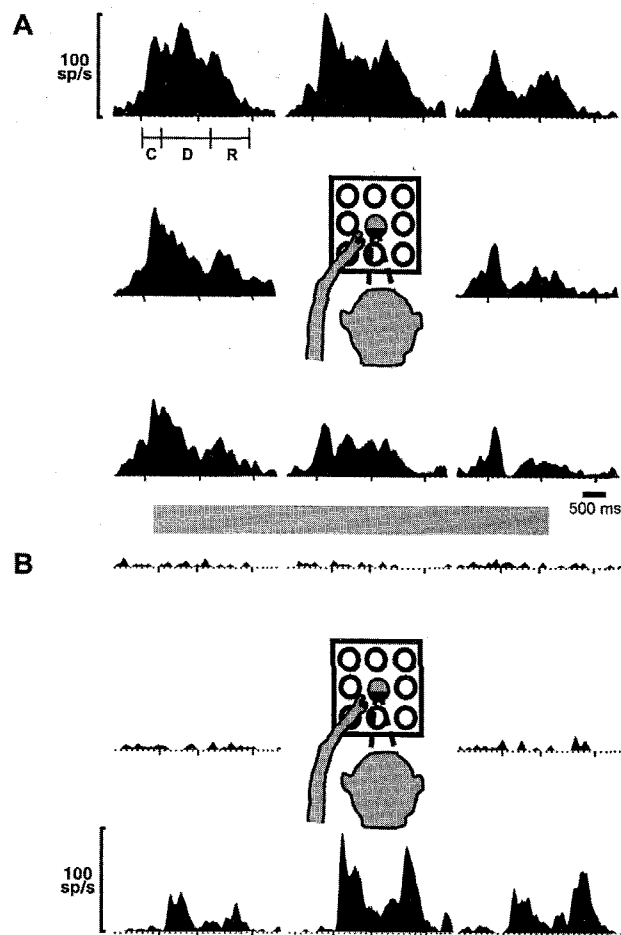


FIGURE 29.1 (A) Response of a PRR neuron during reaches to the remembered location of an auditory stimulus. (B) Response of a PRR neuron during reaches to the remembered location of a visual stimulus. Shown in each case are a schematic of the monkey's initial hand and eye position and a PRR response profile. Circles indicate the relative position of a touch-sensitive button assembly. Each assembly contained light-emitting diodes, which produced visual stimuli, and a speaker, which produced an auditory stimulus. The gray circle in the assembly indicates the button that the monkey pressed initially, and the black circle indicates the button that the monkey fixated; the converging lines indicate the direction of the monkey's gaze. Following presentation of a sensory stimulus from one of the assemblies, monkeys reached and pressed the button in which the stimulus originated. The response profiles are arranged as a function of target location, and neural activity is represented by spike-density histograms. The histograms are aligned relative to the onset of the sensory cue. The gray bar indicates the time of cue onset and the duration of the cue. Tic interval = 100 ms. In A, C, D, and R indicate the times of the cue, delay, and reach periods, respectively. (Modified with permission from Cohen et al., 2002.)

seen in Figure 29.1 by comparing the response profile of a PRR neuron generated during the auditory task (Fig. 29.1A) with one generated during the visual task (Fig. 29.1B). To quantify these differences, we calculated the amount of information related to target

location that is conveyed in the firing rate of PRR neurons during different epochs of the delayed reach task (Cohen et al., 2002). The advantage of this information analysis is that it provides a continuous measure (Cover & Thomas, 1991) of the relationship between neural activity and stimulus-target location. We found that during delayed reaches to visual targets, the firing rate of PRR neurons contained the same amount of information, with respect to target location, throughout the task. In contrast, the amount of information contained in the firing rate of PRR neurons during delayed reaches to auditory targets was initially less than that seen during delayed reaches to visual targets. However, as the trial evolved, the amount of information increased, by the reach period becoming equivalent to the amount coded during visual trials (Fig. 29.2). We interpret these data to suggest that the quantity being encoded in the firing rate of PRR neurons is dynamic and changes as the sensory, cognitive, or motor demands of the task change (Cohen et al., 2002).

This form of dynamic coding of different aspects of a task has been seen in other PPC studies. For instance, in one study, a location on a visual object was cued briefly, the object was then rotated, and the monkey then saccaded to the remembered location of the cue (Sabes, Breznen, & Andersen, 2002). LIP neurons initially coded aspects of the visual stimulus, but as the task evolved, LIP activity became more correlated with the direction of the planned saccade. Similarly, during a saccade task in which the reward and target probabilities were altered, LIP neurons initially coded the monkey's expectancy regarding reward amount or target location, but during later periods of the task, LIP activity became more correlated with the location of the saccade target itself (Platt & Glimcher, 1999). In a recent study, monkeys were trained to judge the motion of moving dots on a visual display and to saccade in the direction of the motion (Shadlen & Newsome, 1996, 2001). LIP activity was initially modulated by the monkey's judgment of motion direction but not in later epochs of the task, when the monkeys had selected a saccadic target.

A common spatial representation in areas LIP and PRR

The reference frame of LIP and PRR activity has been studied by asking monkeys to make movements (saccades or reaches) from different initial starting positions. If neural activity is coded in the reference frame of the body part that is shifted, then the target location that elicits the maximal response from a neuron should shift as the initial starting position of the body part is

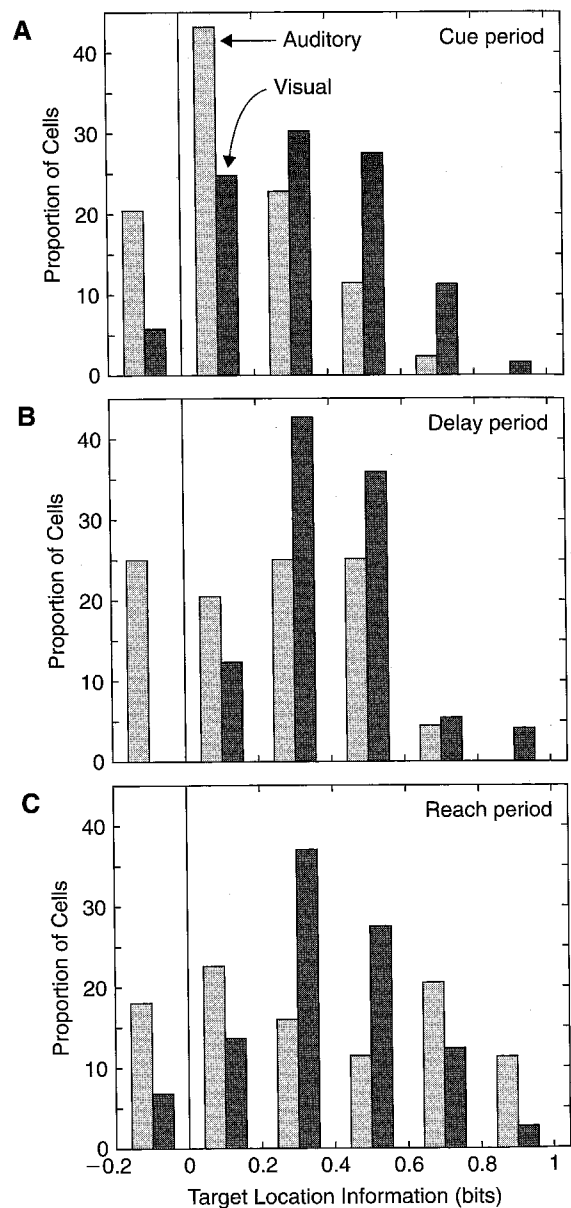


FIGURE 29.2 Distribution of target-location information for 44 PRR neurons that were recorded during delayed reaches to auditory targets and 67 PRR neurons that were recorded during delayed reaches to visual targets. Target-location information is shown for the cue (A), delay (B), and reach (C) periods. Target-location information is a non-parametric index of a neuron's spatial selectivity (Cohen et al., 2002; Cover & Thomas, 1991; Gnadt & Breznen, 1996; Grunewald et al., 1999). The gray bars indicate the distribution of target-location information for auditory-tested PRR neurons and the black bars indicate the distribution for visually-tested PRR neurons. (Modified with permission from Cohen et al., 2002.)

changed. If activity is not coded in that particular reference frame, then the responses of the neurons should be invariant to the shifts in body position.

For instance, LIP neurons code the location of a visual target in an eye-centered reference frame

(Andersen, Bracewell, Barash, Gnadt, & Fogassi, 1990; Brotchie, Andersen, Snyder, & Goodman, 1995; Snyder, Grieve, Brotchie, & Andersen, 1998). In this eye-centered reference frame, the location of a visual stimulus that maximally excites a LIP neuron changes as the monkey's eye position changes (Fig. 29.3A). Do LIP neurons that are responsive to auditory stimuli also code the location of auditory targets in an eye-centered reference frame? Because LIP neurons are involved in the planning of saccades to both auditory and visual stimuli (Grunewald et al., 1999; Linden et al., 1999; Mazzoni et al., 1996; Stricanne et al., 1996), a reasonable hypothesis would be that LIP neurons code the location of an auditory target in the same reference frame as visual targets, an eye-centered reference frame. To test this hypothesis, monkeys were placed in a darkened room and taught to saccade to the remembered locations of auditory stimuli from different initial fixation points (Stricanne et al., 1996). We examined LIP activity during the delay period that followed auditory-stimulus offset but preceded the eye movement. A general linear model tested whether the pattern of neural activity could be attributed to (1) the effect of auditory-target location relative to the monkey's initial eye position or (2) the effect of auditory-target location relative to the monkey's head. If the first variable was significant ($P < 0.05$), that would indicate that LIP activity coded auditory-target location in an eye-centered reference frame (Fig. 29.3A). In contrast, if the second variable was significant, that would suggest that LIP activity was coded in the original head-centered reference frame (Fig. 29.3B) (Blauert, 1997; Cohen & Knudsen, 1999; Middlebrooks & Green, 1991). This possibility, however, is also consistent with the hypothesis that LIP activity codes auditory-target location in a body- or world-centered reference frame; future experiments are needed to address this issue directly. Finally, if both variables were significant, that result would be consistent with the hypothesis that LIP activity codes auditory-target location in a reference frame that is intermediate between a head-centered and an eye-centered reference frame (Fig. 29.3C).

Consistent with the role of LIP in eye-movement planning, we found that a significant population (44%) of LIP neurons codes the location of an auditory target in an eye-centered reference frame. Also, 33% of the neurons coded auditory-target location in a head-centered reference frame. The remaining neurons appeared to code auditory-target location in an intermediate reference frame. The observation that some LIP neurons code auditory-target locations in head-centered and intermediate coordinates is important and suggests that area LIP, and perhaps the PPC in

general, may be directly involved in reference-frame transformations; this concept is discussed in more detail later in the chapter.

We have also examined the reference frame in which PRR neurons code reaches to visual targets (Batista, Buneo, Snyder, & Andersen, 1999). In this study, we examined two alternative hypotheses. First, since PRR neurons code reaches (Battaglia-Mayer et al., 2000; Calton et al., 2002; Eskandar & Assad, 1999; Galletti et al., 1993, 1995, 1996, 1997, 1999, 2001; Johnson et al., 1996; Snyder, Batista, et al., 1998; Snyder et al., 1997, 2000), a likely hypothesis would be that they code the location of visual targets in the reference frame of the motor effector, a reference frame that is based on the difference between initial and final hand position (a limb-centered reference frame; Fig. 29.3E). The second hypothesis that we explored was that PRR neurons code visual reach targets in an eye-centered reference frame (Fig. 29.3A). We explored this reference frame to test the hypothesis that if movement-planning areas in the PPC code in a similar reference frame, PRR activity should be in the same eye-centered reference frame as LIP activity.

These two hypotheses were examined by having monkeys participate in variants of a delayed-reach task to visual targets (see Fig. 29.4). In one variant, monkeys made delayed reaches from different initial-hand positions but maintained the same fixation point. If PRR activity is coded in a limb-centered reference frame (Fig. 29.3E), then the location that maximally excites PRR neurons should shift with changes in initial-hand position. In the second variant, monkeys made delayed reaches from different fixation points but maintained the same initial-hand position. If PRR activity is coded in an eye-centered reference frame (Fig. 29.3A), then the location that maximally excites PRR neurons should shift with changes in initial-eye position.

An example of a PRR neuron that was tested using this paradigm is shown in Figure 29.4. As can be seen, when the monkey made reaches to visual targets from different initial-hand positions, the peak location of the response profile of the neuron was unaltered. In contrast, when the monkey made identical reaches from different fixation points, the peak location of the response profile shifted with eye position. This neuron is typical of the vast majority of PRR neurons and, along with the remaining neurons studied, indicates that PRR neurons code in a format consistent with an eye-centered reference frame for reaches to visually cued locations.

In a separate study, we examined the reference frame of PRR neurons during delayed reaches to auditory targets. Based on the aforementioned results, we

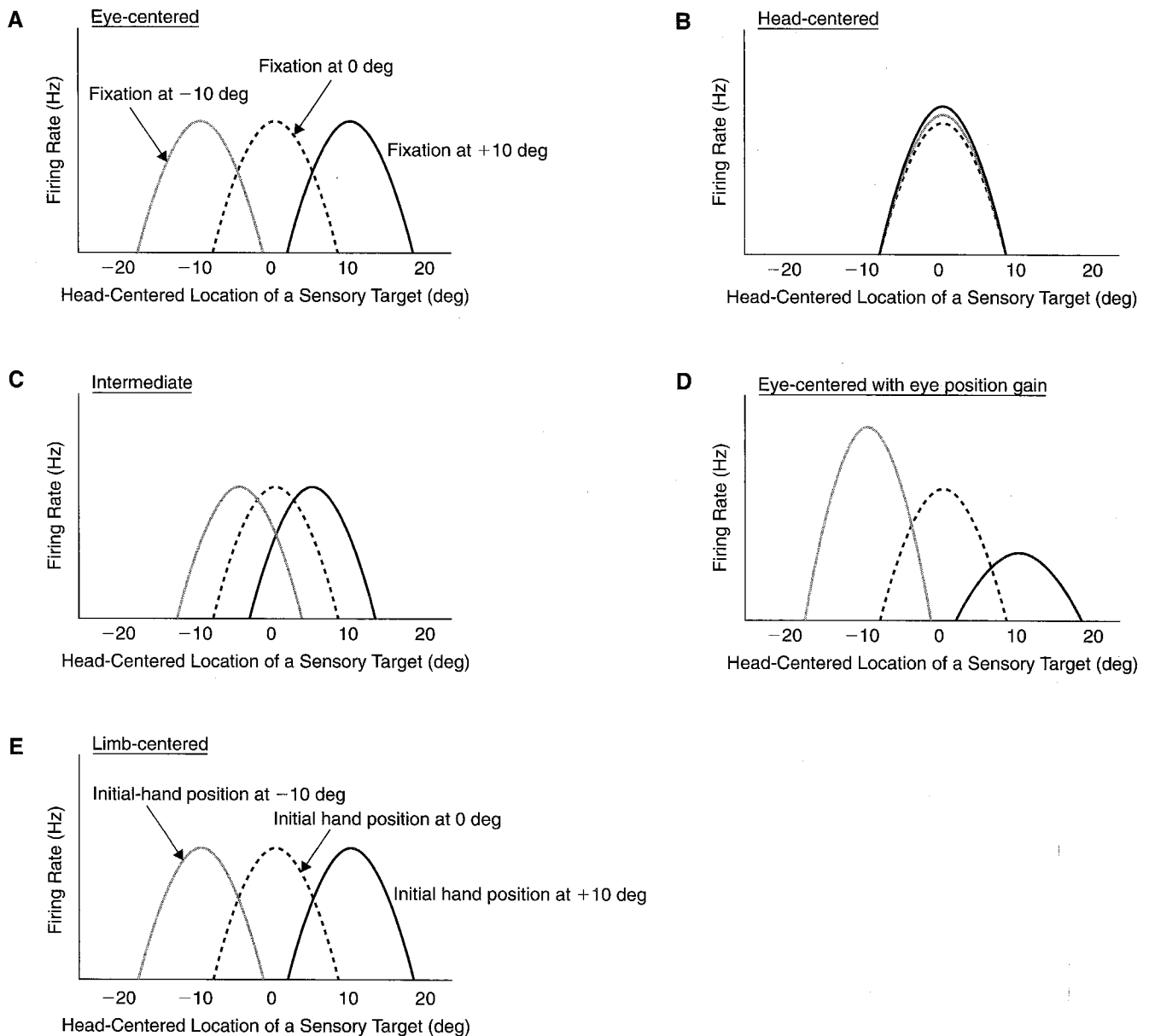


FIGURE 29.3 Schematic of different reference frames. The locations of sensory targets along the abscissa are plotted relative to the observer's head. Hypothetical response profiles in each plot are represented by the bell-shaped curves. (A) If a neuron codes the location of a sensory target in an eye-centered reference frame, then the peak location of the response profile shifts with eye position. For example, a +10-degree shift of eye position would shift the peak of the response profile by +10 degrees. (B) If a neuron codes the location of a sensory target in a head-centered reference frame, then the peak location of the response profile does not shift with eye position. The positions of the three response profiles are offset slightly for visual clarity. (C) If a neuron codes the location of a sensory target in an intermediate reference frame, the peak location of the response profile shifts with eye position. However, the magnitude of the shift is less than the change in eye position. In the hypothetical example shown, a +10-degree shift of eye position shifts the peak of the response profile by only +5 degrees. (D) If a neuron codes the location of a sensory target in an eye-centered reference frame that is modulated by eye position gain, then the peak of the response profile shifts with eye position. Additionally, the magnitude of the response should change with eye position. So, in the hypothetical example shown, a +10-degree shift of eye position shifts the response profile by +10 degrees and decreases the magnitude of the response by 50%. In contrast, a -10-degree shift in eye position shifts the peak response by -10 degrees and increases the magnitude of the response by 50%. For panels A-D, the hypothetical response profile obtained at a fixation point of -10 degrees is plotted in gray, the one at a fixation point of 0 degrees is represented by a dashed line, and the one at a fixation point of +10 degrees is plotted in black. (E) If a neuron codes the location of a sensory target in a limb-centered reference frame, then the peak location of the response profile shifts with initial-hand position. The hypothetical response profile obtained at an initial-hand position of -10 degrees is plotted in gray, the one at an initial-hand position of 0 degrees is represented by a dashed line, and the one obtained at an initial-hand position of +10 degrees is plotted in black.

Different Initial-Hand Positions

Different Eye Positions

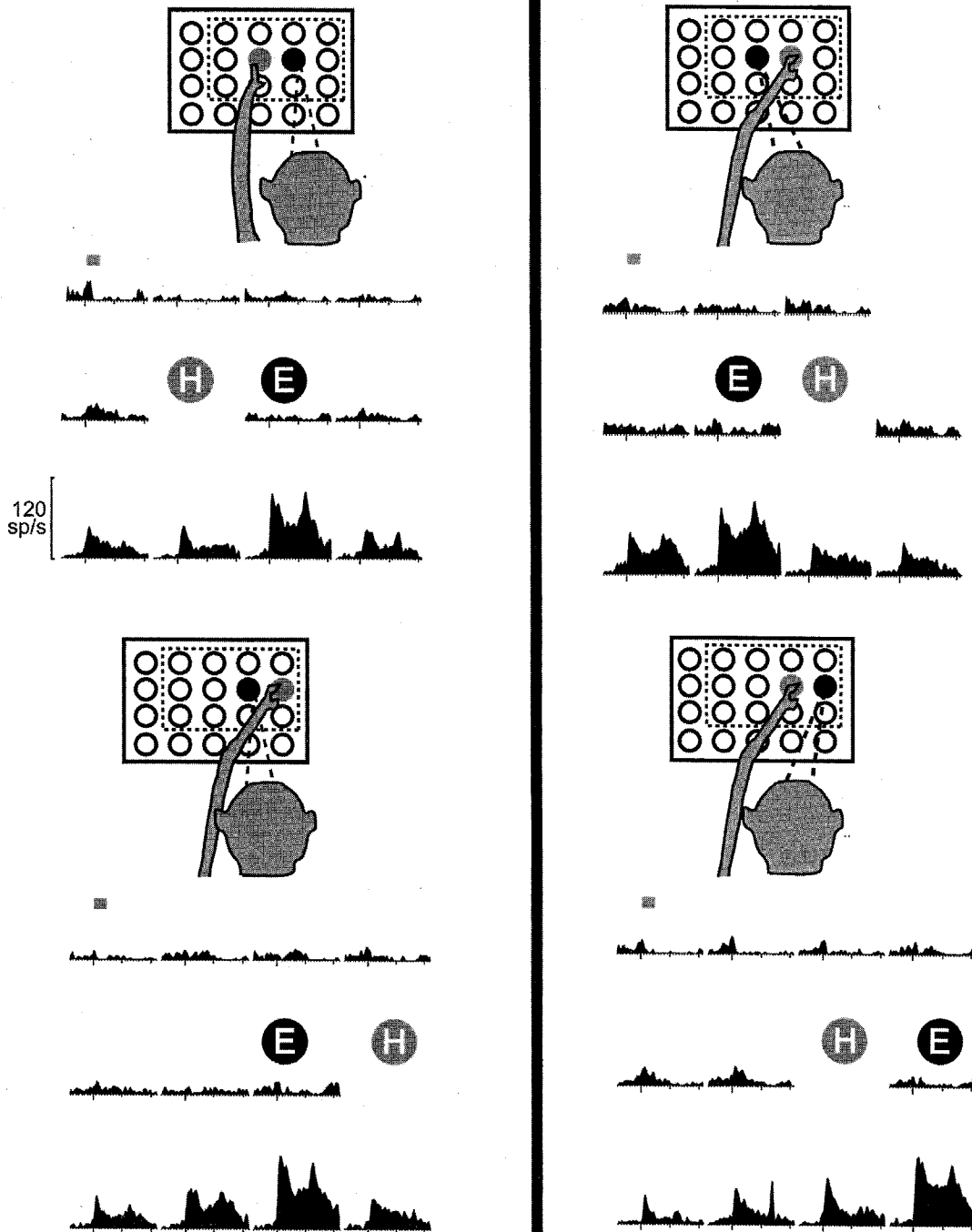


FIGURE 29.4 Example of a PRR neuron that codes reaches to visual targets in an eye-centered reference frame. Each panel in the figure contains a schematic of the monkey's four different variations of initial-hand and eye positions that were employed during this reach task. In each schematic, the circles indicate the relative position of a button assembly that contained two LEDs and a touch-sensitive button, and the dotted square outlines a grid of potential sensory-target locations. Black circle indicates the button that the monkey fixated; the converging line indicates the direction of the monkey's gaze. Gray button indicates the button that the monkey initially pressed. Beneath each schematic is a PRR response profile that was generated from data obtained when the monkey was participating in the variant of the reach task shown in the schematic. The response profiles are arranged as a function of target location, and neural activity is represented by spike density histograms. The histograms are aligned relative to the onset of the sensory cue. The circled E and circled H above the spike-density histograms indicate the location of the monkey's eye position and initial-hand position, respectively. Gray bar indicates the time of cue onset and the duration of the cue. On the left are shown two response profiles generated with the same eye position but different initial-hand positions. On the right are shown two response profiles generated with the same initial-hand position but different eye positions. When eye position varied, the peak of the response profile shifted. In contrast, when initial-hand position varied, the response profiles did not shift. Tic interval = 100 ms.

predicted that during this auditory reaching task, PRR neurons should also code the location of a sound in an eye-centered reference frame. To test this prediction, we placed monkeys in a darkened room and trained them to make delayed reaches to the remembered locations of auditory stimuli from different initial-hand positions and from different fixation points (Cohen & Andersen, 2000). If PRR auditory activity occurs in a limb-centered reference frame (Fig. 29.3E), then the peak of a PRR response profile should shift with changes in initial hand position. If PRR activity occurs in an eye-centered reference frame (Fig. 29.3A), then the peak of a PRR response profile should shift with changes in the monkey's fixation point.

Figure 29.5 shows the response profiles of a PRR neuron that were obtained while a monkey participated in this delayed-reach task to auditory targets. Much as for the neuron illustrated in Figure 29.4, the peak of this neuron's response profile shifted with changes in eye position and was invariant to changes in initial-hand position, suggesting that this neuron coded the location of an auditory target in an eye-centered reference frame.

Interestingly, in some PRR neurons the eye and initial-hand position affected PRR activity in a complex manner. An example of a complex interaction between eye and initial-hand position is shown in Figure 29.6. When the monkey shifted eye position from left to right, the peak of the response profile shifted from the right of the monkey's initial-hand position to the left of the animal's initial hand position. In contrast, when the monkey shifted initial-hand position from left to right, the peak of the response profile shifted moderately to the right.

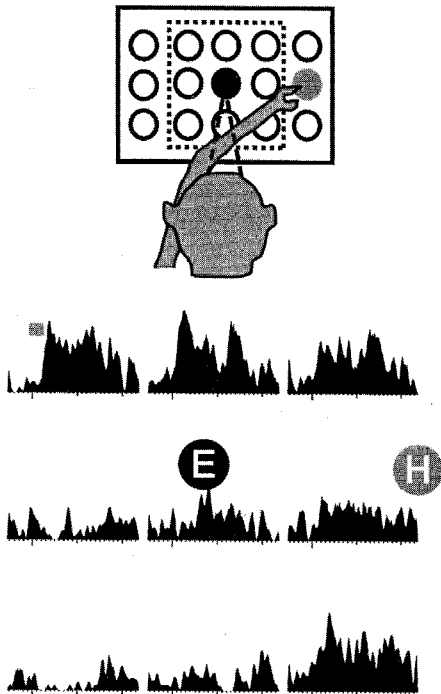
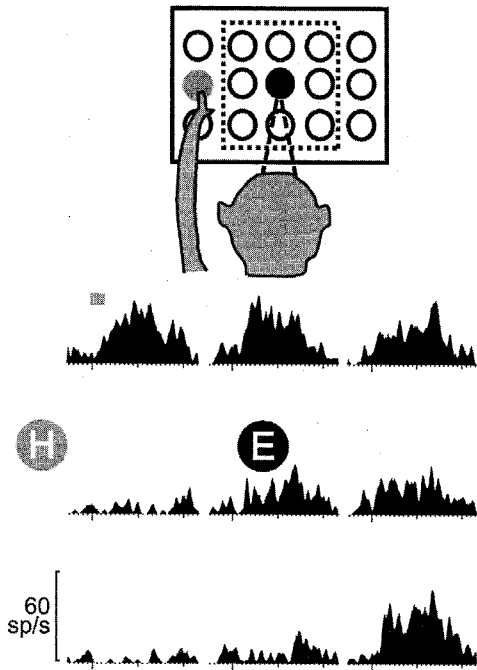
To quantify the effect that initial-hand and eye position had on PRR activity during reaches to auditory targets, we examined the firing rate during the delay period. Activity during this period was examined because there was no auditory stimulus present and the monkey was not executing a reach. In a first analysis, we correlated the response profiles that were generated when the monkey made reaches from different eye positions and the response profiles that were generated when the monkey made reaches from different initial-hand positions. We found that, in a significant number of PRR neurons, the correlation coefficient between the response profiles generated from the different eye positions was less than the correlation coefficient between the response profiles generated from the different initial hand positions. In other words, PRR activity was significantly more sensitive to changes in eye position than to changes in initial-hand position.

A second analysis examined directly whether this sensitivity to eye position was equivalent to the hypothesis

that PRR neurons coded in an eye-centered reference frame. To test this hypothesis, we calculated the cross-correlation coefficient between the two response profiles generated with different eye positions. The cross-correlation coefficient was generated by calculating the correlation coefficient between the two response profiles when one response profile was held constant and the other was shifted horizontally, relative to the first response profile; the curves were shifted horizontally because the two eye positions used in this study varied along the horizontal dimension. Since the two eye positions were located 18 degrees to the left and 18 degrees to the right of the central fixation position, the response profiles were shifted either by -36 degrees, -18 degrees, 0 degrees, $+18$ degrees, and $+36$ degrees. After shifting the response profiles, we correlated them in the region of overlap. The optimal shift was the one with the maximum correlation coefficient. In this analysis, the two response profiles were aligned, relative to eye position, when one response profile was shifted by -36 degrees. Thus, if a cell had an optimal shift of -36 degrees, it aligned best in an eye-centered reference frame. In contrast, a 0 -degree optimal shift suggested that the activity of a PRR neuron was insensitive to eye position. Neurons with this optimal-shift value may be in another reference frame, such as head-centered. Intermediate shift values indicated alignment in intermediate frames of reference. We found that a significant proportion (42%) of PRR neurons coded the location of an auditory stimulus in an eye-centered reference frame. For 45% of PRR neurons, changes in initial-hand position and changes in eye position did not affect the location of the peak response. These neurons most likely coded auditory-target location in a head-centered reference frame (Fig. 29.3B), although, as with LIP auditory activity, this proposition needs to be addressed directly. The remaining population of neurons (13%) appeared to code auditory-target location in a reference frame that was intermediate between a head-centered and an eye-centered reference frame (Fig. 29.3C). As with our observations in area LIP, the observation that there are PRR neurons with head and intermediate reference frames is indicative of a direct role for the PPC in reference frame transformations, as will be discussed in greater detail later in this chapter.

We have highlighted analyses of neural activity during the delay period of saccade and reach tasks. However, our observations are not dependent on analyses of delay-period activity. We have found that, during the presentation of the auditory target and during the reach, a significant number of PRR neurons code in a format that is more consistent with eye-centered coordinates

Different Initial-Hand Positions



Different Eye Positions

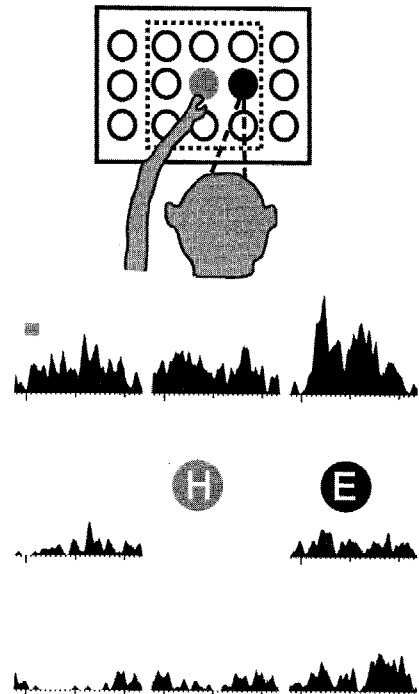
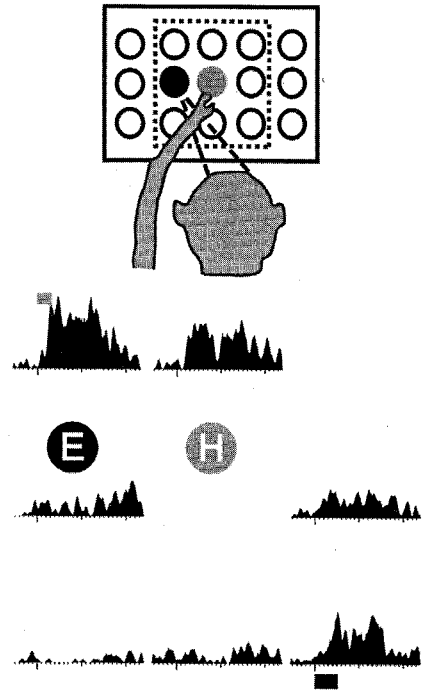
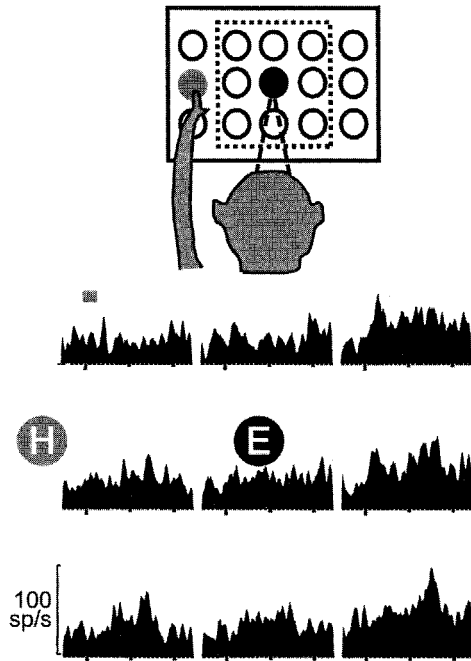


FIGURE 29.5 Example of a PRR neuron that codes reaches to auditory targets in an eye-centered reference frame. Same conventions as those described in Figure 29.4, except that auditory rather than visual targets were used. When eye position varied, the peak of the response profile shifted. In contrast, when initial-hand position varied, the response profiles did not shift. Tic interval = 100 ms.

Different Initial-Hand Positions



Different Eye Positions

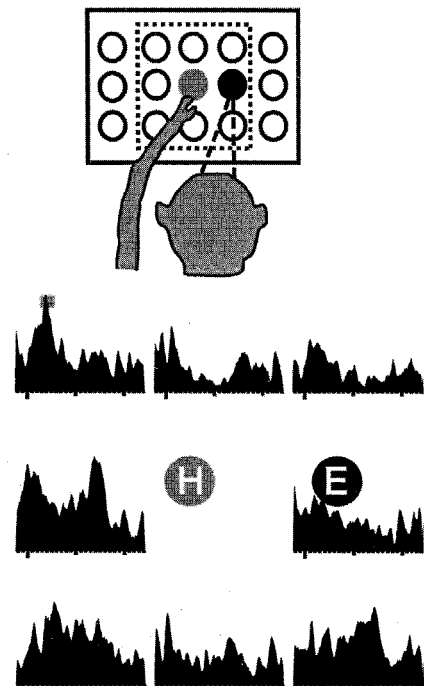
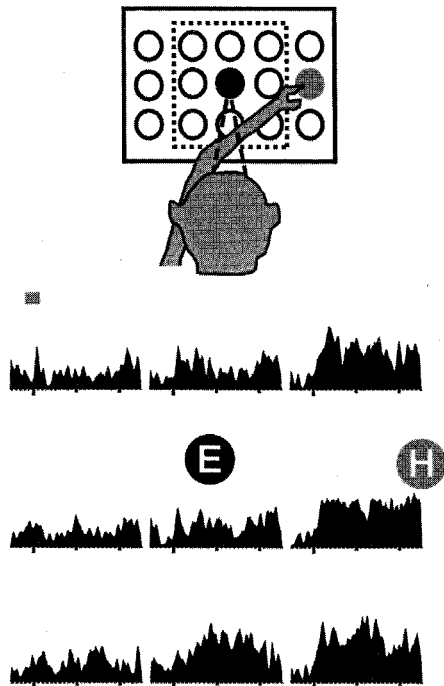
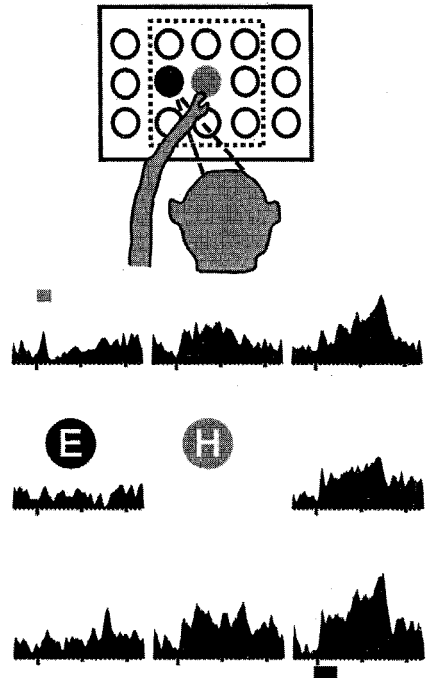


FIGURE 29.6 Example of a PRR neuron that codes reaches to auditory targets in a reference frame that is dependent on both eye position and initial-hand position. Same conventions as those described in Figure 29.4, except that auditory rather than visual targets were used. When eye position varied, the peak of the response profile shifted. In contrast, when initial-hand position varied, the response profiles did not shift. Tic interval = 100 ms.

than arm-centered coordinates (Y. E. Cohen & R. A. Andersen, unpublished observations).

We interpret these reference-frame studies to suggest that a significant proportion of LIP and PRR activity codes the location of a sensory target in a common eye-centered reference frame. This reference frame is considered abstract, insofar as it is (1) not directly linked to the reference frame of the sensory target and (2) not linked to the eventual motor effector. Because the aforementioned studies examined only how PPC neurons code the locations of auditory or visual targets, it will be important to determine whether LIP and PRR neurons that respond to both auditory and visual targets code these sensory targets in the same reference frame.

LIP and PRR activity is further modulated by such factors as head, eye, body, initial hand, and body position (see Fig. 29.3D) (Battaglia-Mayer et al., 2000; Brotchie et al., 1995; Buneo, Jarvis, Batista, & Andersen, 2002; Cohen & Andersen, 1998; Duhamel, Bremmer, BenHamed, & Graf, 1997; Galletti et al., 1995; Snyder, Grieve, et al., 1998). An example of a PRR neuron that is gain modulated is shown in Figure 29.7. The response profiles in this figure were generated from data obtained when a monkey made delayed auditory reaches. The overall response or gain of the neuron was significantly modulated by changes in the monkey's fixation point. When the monkey's fixation point was to the left, the neuron's response was robust, but when the monkey's fixation point was to the right, the response of the neuron was minimal. In contrast, changes in initial-hand position did not substantially change the level of responsiveness of the neuron.

What is the function of these gain fields? Several independent computational studies indicate that gain fields and eye-centered representations form a distributed representation of target locations in different reference frames (Bremmer, Pouget, & Hoffmann, 1998; Deneve, Latham, & Pouget, 2001; Xing & Andersen, 2000a, 2000b; Zipser & Andersen, 1988). As a result, cortical areas that receive input from the PPC are thought to be capable of "reading out" target locations in a reference frame that is appropriate for the computations mediated by that area. For instance, the head-centered location of a sensory target can be computed by convergent inputs from cells that codes the eye-centered location of the target with eye-position gain. This convergence may occur in ventral intraparietal area, a PPC region that contains a substantial population of neurons that code visual targets in a head-centered reference frame (Duhamel et al., 1997), or in a small population of parieto-occipital neurons (Galletti et al., 1993). Combining the eye-centered location of a

sensory target with signals about initial-hand position can create a limb-centered reference frame. This computation may occur in area 5, a region of the superior parietal cortex that is involved in programming reaches (Kalaska, 1996). Neurons in this parietal area code the location of visual targets in coordinates intermediate between eye and limb coordinates (Buneo et al., 2002).

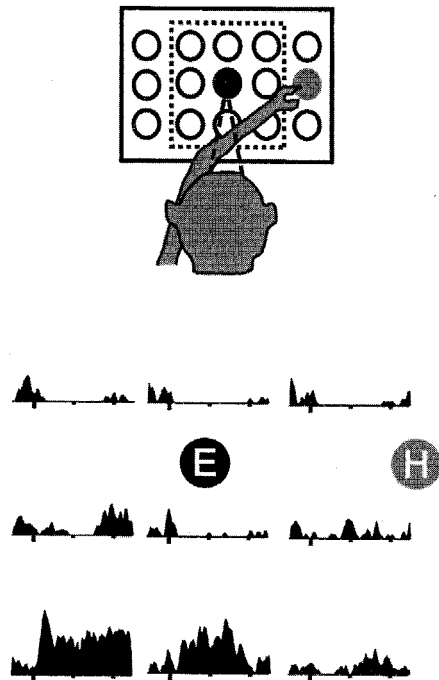
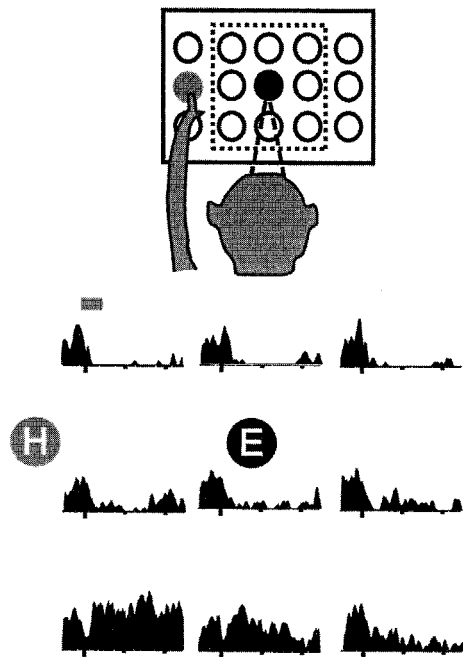
These observations at the level of single neurons in area LIP and PRR appear not to be limited to the monkey PPC. Functional homologues of eye-centered representations have been reported in the human PPC (Serenio, Pitzalis, & Martinez, 2001). Also, imaging studies have indicated that neural activity in the human PPC is also gain modulated (Baker, Donoghue, & Sanes, 1999; DeSouza et al., 2000). Finally, psychophysical studies have demonstrated that humans code reaches to auditory, visual, and proprioceptive stimuli in eye-centered coordinates (Bock, 1986; Enright, 1995; Henriques, Klier, Smith, Lowy, & Crawford, 1998; Pouget, Ducom, Torri, & Bavelier, 2002).

Are eye-centered representations of auditory stimuli created in the PPC?

Are eye-centered representations of auditory targets created in the PPC? Or are they generated in areas that project to the PPC? One way to address this issue is to examine the reference frame of auditory activity from brain areas that project either directly to the PPC, such as area Tpt in the superior temporal sulcus, or indirectly to the PPC, such as core regions of the auditory cortex or the inferior colliculus (Andersen, Asanuma, Essick, & Siegel, 1990; Kaas & Hackett, 1998; Leinonen, Hyvärinen, & Sovijarvi, 1980; Lewis & Van Essen, 2000; Pandya & Sanides, 1973; Seltzer & Pandya, 1984, 1994; Sparks & Hartwich-Young, 1989). In all three of these brain areas, auditory neurons code the location of a sound in a head-centered reference frame that is also modulated by changes in eye position (Groh, Trause, Underhill, Clark, & Inati, 2001; Trause, Werner-Reiss, Underhill, & Groh, 2000; Wu & Andersen, 2001). The results of the Tpt study are particularly telling, since this area is the primary source of auditory input to the PPC (Kaas & Hackett, 1998; Leinonen et al., 1980; Lewis & Van Essen, 2000; Pandya & Sanides, 1973; Seltzer & Pandya, 1984, 1994). Insofar as the auditory areas that lead to the PCC represent sensory-target locations in a head-centered reference frame, the PPC may be a locus for transforming head-centered representations of auditory targets into eye-centered representations.

A caveat to this interpretation is that the reference frame of the neurons in these three auditory areas was determined through behavioral tasks that were

Different Initial-Hand Positions



Different Eye Positions

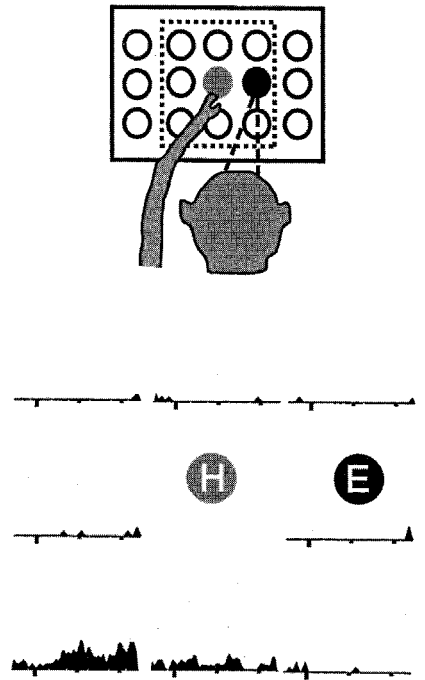
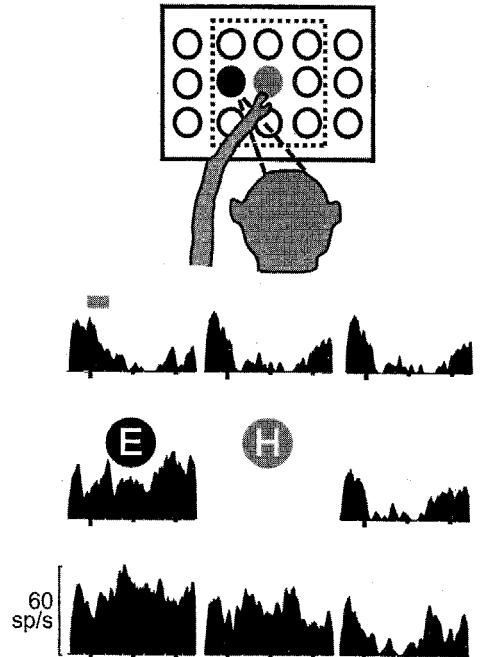


FIGURE 29.7 Example of a PRR neuron that codes reaches to auditory targets in a head-centered reference frame and is substantially gain-modulated by eye position. Same conventions as those described in Figure 29.4. When eye position varied, the magnitude or gain of the response varied substantially. In contrast, when initial-hand position varied, the gain of the response was essentially constant.

somewhat different from those used in the PPC studies. In the inferior colliculus (Groh et al., 2001), auditory cortex (Trause et al., 2000), and Tpt (Wu & Andersen, 2001) studies, monkeys were not required to execute any movements toward the location of the auditory targets. Instead, they listened passively to band-limited noise while maintaining their gaze at different locations. The degree to which a neuron's reference frame depends on the behavioral task is not clear. It is not inconceivable that the reference frame of neurons is task dependent and reflects the needs of the ongoing task (Colby, 1998). If so, then the reference frame of neurons in these auditory areas may be eye-centered during saccade or reach tasks. Direct experimental work in the future should address this interesting issue.

Computational studies also point to the PPC as being a locus for the transformation of head-centered representations of auditory stimuli into eye-centered representations (Deneve et al., 2001; Xing & Andersen, 2000a, 2000b). These studies used three-layer neural networks to probe the mechanisms underlying reference-frame transformations. In the Xing and Andersen model, the first layer, or the input layer, contained a map of visual-target location in an eye-centered reference frame, a map of auditory-target location in a head-centered reference frame, and a representation of head and eye position. The second, "hidden" layer of the network received input from the first input layer and sent connections to the third (output) layer. The output layer was trained to represent target locations in a variety of reference frames, such as eye-centered, head-centered, and/or body-centered.

An analysis of the computational units in the hidden layer of the network following training revealed important insights. First, these units often represented target locations in an intermediate reference frame. For instance, when the network was trained to convert the head-centered representation of an auditory target into an eye-centered representation, a proportion of the units represented auditory-target location in a reference frame intermediate between head and eye. Second, they often coded target location in an eye-centered (or intermediate) reference frame that was modulated by eye and head position. For instance, if the network was trained to code target location in a body-centered reference frame, the units in the hidden layer would code the target location in an eye-centered reference frame that was modulated by eye-position and head-position gain signals. These two observations suggest that cortical areas involved in coordinate transformations utilize both gain fields and intermediate reference frames as mechanisms to convert sensory representations from one reference frame to another.

At least two factors seem likely to contribute to the construction of intermediate reference frames in our network. First, the auditory response fields of the units in the hidden layer were relatively large and asymmetrically shaped, much like the auditory response fields seen in LIP and PRR neurons (Cohen & Andersen, 2000; Stricanne et al., 1996). The second factor was the nonlinear sigmoidal interaction between the eye-position signals and the representations of target location. The combination of these two factors resulted in a partially shifted response field, one that had an intermediate reference frame.

Other modeling studies also illustrated the importance of intermediate reference frames in coordinate transformations (Deneve & Pouget, 2003; Deneve et al., 2001). These studies, like the one mentioned earlier, used a three-layer neural network. However, unlike our network, they allowed for both feed-forward and feedback connections between adjacent layers and lateral connections within a layer and coded target position with a different formulation, namely, a basis set of Gaussian functions. Despite the differences, the computational units in the hidden layer also had gain fields and represented information in an intermediate reference frame.

The finding that gain modulation and intermediate reference frames are seen in PPC neurons (Battaglia-Mayer et al., 2000; Brotchie et al., 1995; Buneo et al., 2002; Cohen & Andersen, 1998; Duhamel et al., 1997; Galletti et al., 1995; Snyder, Grieve, et al., 1998; Stricanne et al., 1996) and in computational models of reference frame transformations (Deneve et al., 2001; Xing & Andersen, 2000a, 2000b; Zipser & Andersen, 1988) supports the notion that the PPC is part of a network for reference-frame transformations. However, there is no direct neurophysiological evidence linking these computational mechanisms with reference-frame transformations. It is important to establish a causal neurophysiological link between gain modulation, intermediate frames of reference, and coordinate transformations to determine directly whether the PPC uses these mechanisms in coordinate transformations.

Advantages of a common reference frame

Although an eye-centered representation of target location in the PPC may represent an intermediate stage of a network devoted to reference-frame transformations, it is also possible that it may be a prerequisite stage in transforming representations of sensory stimuli from sensory-based coordinates into motor-based coordinates that are useful for programming a movement (Flanders et al., 1992; Ghilardi et al., 1995; Kalaska &

Crammond, 1992; Snyder, 2000; Soechting & Flanders, 1989a, 1989b). Another possibility is that it coexists in parallel with these other processes (Graziano, 2001; Snyder, 2000) and is used for specific functions or tasks, such as hand-eye coordination. For example, a common reference frame for encoding the locations of sensory targets may be an efficient manner in which to represent target locations. Since the world contains stimuli of different modalities, a common representation (Batista et al., 1999; Sabes & Jordan, 1997) may facilitate the process by which the brain represents their location and computes the motor plans that are needed to direct an effector toward them. Also, during natural behaviors, we often direct multiple effectors toward a common location. For instance, we often direct our gaze and reach to a common location. Given this, it is reasonable to predict that both area LIP and PRR would be involved in such a task, and a common reference frame may facilitate the coordination and communication between these two areas.

Why, though, is there an eye-centered representation? Because this reference frame is abstract and not tied to stimulus modality or motor effector, it can, in principle, occur in any of a number of different reference frames. We speculate that an eye-centered representation is used because the sensory modality with the highest spatial acuity is vision. Many aspects of auditory perception are modulated by eye position or the location of a visual stimulus (Lewald, 1997, 1998; Lewald & Ehrenstein, 1996; Pouget et al., 2002; Shams, Kamitani, & Shimojo, 2000), and vision plays a key role in calibrating the auditory system's capacity to localize a sound source (King, Schnupp, & Doubell, 2001; Knudsen, 1999; Zwiers, Van Opstal, & Cruysberg, 2001).

Conclusions

The PPC appears to be central to computations that underlie coordinate transformations. Many area LIP and PRR neurons code auditory targets in eye-centered coordinates, similar to the visual representations in these areas. These eye-centered response fields are gain modulated by eye and head position signals (LIP) and eye and limb position signals (PRR). These gain effects allow the population to be read out in a variety of coordinate frames; that is, it can be considered a distributed representation, simultaneously representing locations in many reference frames. The observation of PPC neurons with intermediate reference frames also suggests that the PPC is a locus for coordinate transformations. The common representation in PRR and LIP may be used to facilitate different aspects of goal-oriented behavior. The studies reviewed in this chapter

emphasize the role of the PPC as an interface between sensation and action and as an area in which cognitive intermediates of the sensorimotor transformation, such as reference-frame transformations, occur.

Several lines of research are opened by these studies. For instance, is this common reference frame found only in area LIP and PRR, or is it utilized by other cortical areas involved in goal-orientated behavior? Another important question to consider is whether this common reference frame can be extended to other stimulus modalities and other types of movement plans. For instance, might LIP and PRR neurons code somatosensory targets in the same common reference frame as auditory and visual targets? Also, the computational models suggest that neurons with intermediate frames of reference and gain fields are in the middle layer of a network, whereas those with eye-centered representations are in the output layer. How do these observations map onto the anatomical architecture of the PPC? Do PPC neurons with intermediate frames of reference project to those with eye-centered representations? Is there a laminar specificity for neurons with different frames of reference? Examinations of the functional connectivity of the PPC with respect to its intrinsic connectivity and its pattern of afferent and efferent connections are important to further elucidate the specific role of the PPC in reference-frame transformations. Finally, how dynamic is this common reference frame? Is this eye-centered representation obligatory, or can it be changed as the demands of the task change? It is possible that tasks that require hand-eye coordination might be more likely to use a common coordinate frame. However, other tasks may not require such a reference frame, and consequently, target locations may be represented in a different manner.

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