INTENTIONAL MAPS IN POSTERIOR PARIETAL CORTEX

Richard A. Andersen and Christopher A. Buneo
Division of Biology, California Institute of Technology, Mail Code 216-76, Pasadena, California 91125; email: andersen@vis.caltech.edu; chris@vis.caltech.edu

■ **Abstract**   The posterior parietal cortex (PPC), historically believed to be a sensory structure, is now viewed as an area important for sensory-motor integration. Among its functions is the forming of intentions, that is, high-level cognitive plans for movement. There is a map of intentions within the PPC, with different subregions dedicated to the planning of eye movements, reaching movements, and grasping movements. These areas appear to be specialized for the multisensory integration and coordinate transformations required to convert sensory input to motor output. In several subregions of the PPC, these operations are facilitated by the use of a common distributed space representation that is independent of both sensory input and motor output. Attention and learning effects are also evident in the PPC. However, these effects may be general to cortex and operate in the PPC in the context of sensory-motor transformations.

INTRODUCTION

The posterior parietal cortex (PPC) has traditionally been viewed as a sensory "association" area, associating different modalities and having higher-level sensory functions such as spatial attention and spatial awareness. In this review, we highlight a new view of the PPC that is emerging. It is proposed that the PPC, rather than serving a purely sensory or motor role, subserves higher-level cognitive functions related to action. Among these higher cognitive functions is the formation of intentions, or early plans for movement. These intentions are anatomically segregated within the PPC, with regions specialized for the planning of saccades, reaches, and grasps. Moreover, these intentions are highly abstract and are evident in the discharge of single neurons even when a specific intention is not carried out.

The different intention-related regions of the PPC appear to participate in operations critical to the earliest stages of movement planning: multisensory integration and coordinate transformations. These functions are facilitated by employing a rather unique, distributed code. The response fields of neurons in at least two regions are in retinal coordinates, independent of both the sensory modality used to

189

cue target locations (i.e., audition vs. vision) and the action that will ultimately be performed (i.e., reaches vs. saccades). However, these retinal fields are also gain modulated by eye, head, and limb positions. As a result, groups of parietal cells do not generally represent space in a single, defined spatial reference frame. Rather, they code locations in a distributed manner, which can be read out by other groups of neurons in a variety of reference frames.

We describe a potential medical application that utilizes the finding that the PPC encodes movement intentions. The intention-related activity in the PPC can, in principle, be used to operate a neural prosthesis for paralyzed patients. Such a neural prosthesis would consist of recording the activity of PPC neurons, interpreting the movement intentions of the subject with computer algorithms, and using these predictions of the subject's intentions to operate external devices such as a robot limb or a computer. We describe preliminary investigations in healthy monkeys that estimate the number of parietal cells needed to operate such a prosthesis (Meeker et al. 2001, Shenoy et al. 1999b). We also describe a recent finding that monkeys can use this intended movement activity to position a cursor on a computer screen just by thinking about a reach movement, without actually generating a reach (D. Meeker, S. Cao, J. W. Burdick & R. A. Andersen, unpublished observations). This result was obtained without extensive training and strongly suggests that we are in fact tapping into the highly abstract neural signals that represent the earliest plans for movement.

THE PPC SUBSERVES COGNITIVE FUNCTIONS RELATED TO ACTION

Many of the deficits observed following lesions of the PPC are consistent with the area playing a high-level, cognitive role in sensory-motor integration. Patients with PPC lesions do not have primary sensory or motor deficits. However, when they attempt to connect these functions, for instance during sensory guided movements, then defects become apparent. Patients with PPC lesions often suffer from optic ataxia; that is, difficulty in estimating the location of stimuli in 3D space, as indicated by pronounced errors in reaching movements (Balint 1909, Rondot et al. 1977). Patients with PPC lesions can also suffer from one or more of the apraxias, a class of deficits characterized by the inability to plan movements (Geshwind & Damasio 1985). These can range from a complete inability to follow verbal commands for simple movements, to difficulty in performing sequences of movements. Patients with parietal lobe damage also have difficulty correctly shaping their hands as they prepare to grasp objects, which again points to a disconnection between the visual sensory apparatus that registers the shape of objects and the motor systems that shape the configuration of the hand (Goodale & Milner 1992, Perenin & Vighetto 1988).

Neglect is another deficit commonly attributed to lesions of the PPC, although there is currently some debate about whether it is damage to the PPC or to the nearby superior temporal gyrus that is the source of this defect (Critchley 1953, Karnath et al. 2001). The hallmark of neglect is the lack of awareness within the

personal and extrapersonal space contralateral to the lesioned hemisphere, with the most profound deficits seen with right hemisphere lesions in right-handed humans.

These clinical results are extremely informative and useful and have helped guide much of the neurophysiological investigation of the PPC. However, to understand the neural mechanisms and circuits within the PPC that are involved in sensory-motor integration requires that the investigator, rather than relying on the happenstance of medical defects, be able to control the parameters of the experiments. Moreover, refined techniques need to be applied. In the case of humans, this has generally taken the form of fMRI studies, and in the case of monkeys, electrophysiological recording and anatomical studies. The monkey has proven to be a good model for the study of the PPC, since sophisticated motor behaviors such as hand-eye coordination are similar in the two species of primates, and there is extensive evidence to suggest that the PPC in both species performs similar functions (Connolly et al. 2000, DeSouza et al. 2000, Rushworth et al. 2001b). Evidence from these studies provides additional support for the concept that the PPC is neither strictly sensory nor motor but rather is involved in high-level cognitive functions related to action (Mountcastle et al. 1975, Andersen 1987, Goodale & Milner 1992). These functions include early-movement planning, particularly the coordinate transformations required for sensory-guided movement. The activity of PPC may also be influenced by spatial attention and learning. However, these functions are general to cortex, and in the PPC appear to operate in the more specific context of sensory-motor operations.

INTENTION

Intention is an early plan for a movement. It specifies the goal of a movement and the type of movement. For instance, "I wish to pick up the coffee cup" specifies both the goal and type of movement. An intention is high level and abstract. For instance, we can have intentions without actually acting upon them. Moreover, a neural correlate of intention does not necessarily contain information about the details of a movement, for instance the joint angles, torques, and muscle activations required to make a movement. As discussed below, intentions are initially coded in visual coordinates in at least some of the cortical areas within the PPC. This encoding is consistent with a more cognitive representation of intentions, specifying the goals of movements rather than the exact muscle activations required to execute the movement.

An intention is also a broad category of cortical functions, which include decision making (Gold & Shadlen 2001) and "motor attention" (Rushworth et al. 2001a). For instance, decision making can be considered a competition between potential movement intentions (Platt & Glimcher 1999). It may also be the case that the earliest intentions sit atop a sequence of increasingly more specific movement plans. In the example above, the earliest intention may reflect the desire to grasp the cup, with further specifications including which limb (right or left), the trajectory of the movement to avoid obstacles, the coordination of eye and hand movements, the speed of the movement, etc. Only further research will be

able to resolve which parameters of a movement are coded at which stages in the sensory-motor pathway.

Distinguishing Intention from Attention

The issue of intention versus attention has been most prominent in the study of the PPC, which is perhaps not surprising considering this area is at the interface between sensory and motor systems. Mountcastle and colleagues (1975) first noted neural activity in the PPC related to the behaviors of monkeys. Robinson and colleagues (1978) later argued that these effects could be due to sensory stimulation and attention during movement. In experiments designed to tease apart sensory and movement components of activity, Andersen et al. (1987) found both, which is consistent with a role for this area in sensory-motor transformations.

One common method of separating sensory from motor components is the so-called memory task (Hikosaka & Wurtz 1983) in which an animal is cued as to the location for a movement by a briefly flashed stimulus but must withhold the response until a go signal. Typically, PPC neurons show bursts of activity to the cue and the movement, indicating both sensory- and motor-related activity. However, during the memory period the cells in many parietal areas have persistent activity, even in the dark (Gnadt & Andersen 1988, Snyder et al. 1997). This persistent activity by and large does not represent the sensory memory of the target. This can be demonstrated using tasks in which animals memorize the locations of two stimuli and subsequently make movements to both locations. For eye and arm movements the persistent activity in the delay period for nearly all neurons in the PPC is only present for the next planned movement (Batista & Andersen 2001, Mazzoni et al. 1996a), even though the animals must hold in memory two cued locations. This result indicates that the sensory memory of the target locations is either contained in a very small subset of neurons within the PPC, or in areas outside the PPC, perhaps in the frontal lobe (Tian et al. 2000).

The results of the double movement tasks rule out the coding of a sensory memory in the delay period activity. However, this activity could reflect either the direction of a movement plan or the direction of attention. Experimentally it has been very difficult to distinguish movement planning or preparation from spatial attention. Most studies of attention in monkeys use experimental paradigms that require animals to make eye or limb movements as part of the experimental design, or have the potential artifact of the animal covertly planning these movements. This fact is reason for concern in studies of the dorsal, sensory-motor pathway since there is extensive overlap of circuitry concerned with attention and eye movements, as demonstrated by fMRI experiments in humans (Corbetta et al. 1998). The finding that the locus of spatial attention can affect the metrics of saccades electrically evoked from the superior colliculus (SC) further argues for a very tight coupling of spatial attention and eye movements (Kustov & Robinson 1996). These and other results have led Rizzolatti and colleagues to argue for a motor theory of spatial attention (1994). They propose that spatial attention is an early form of motor preparation, at least for eye movements.

Some investigators have used antisaccade and antireach tasks to separate sensory from movement processing. In these paradigms, animals are trained to make movements in the opposite direction from flashed visual targets. For the case of reaches, activity in the medial intraparietal area (MIP) has been reported to code mostly the direction of the movement, and not the location of the stimulus (Eskandar & Assad 1999, Kalaska 1996). Gottlieb & Goldberg (1999) have reported that the reverse is true in the lateral intraparietal area (LIP) for eye movements, i.e., that cells respond to the stimulus and not the direction of planned movement. However, a recent report by Zhang & Barash (2000) indicates that, after a brief transient linked to the stimulus, most cells in LIP code the direction of the planned eye movement. Moreover, a smaller class of cells encode both the location of the stimulus and the movement plan, which suggests that LIP is involved in the intermediate stages of the sensory-motor transformations required for the antisaccade task. Overall, these antisaccade and antireach results reinforce the idea that PPC cells have both sensory- and movement-related responses, and occupy an intermediate stage in the sensory-motor transformation process.

We recently conducted an experiment specifically designed to separate the effects of spatial attention from those of intention (Snyder et al. 1997). In this experiment, animals attended to a flashed target and planned a movement to it during a delay period, but in one case they were instructed to plan a saccade and in the other a reach (see Figure 1*a*). The only difference in the task during the memory period was the movement the animals were planning to make. We reasoned that if PPC activity reflected a sensory memory or attention, it should be the same in the two conditions, but if it reflected the movement plan it should be different.

Figure 1 shows two intention-specific neurons, one from area LIP (*b*) and one from an area we refer to as the parietal reach region (PRR) (*c*). In this task the monkey plans an eye or an arm movement to the same location in space. The activity of the LIP neuron illustrated in panel (*b*) shows a transient response to the onset of the briefly flashed target. This is followed by activity during the delay period if the animal is planning an eye movement (left histogram), but not if he is planning an arm movement to the same location (right histogram). In contrast, the cell in panel (*c*) shows no activity above baseline in the delay period when the animal is planning an eye movement, but strong activity when he is planning an arm movement. Such results were typical in the PPC: In general, we found that during eye movement planning area LIP was much more active, and during limb movement planning PRR was more active. PRR included MIP, 7a, and the dorsal aspect of the parieto-occipital (PO) area, though MIP was found to have the highest concentration of reach-related neurons. The results from both LIP and PRR argue strongly for a role of the PPC in movement planning.

A subsequent experiment showed that activity in the PPC is also related to the shifting of movement plans, when spatial attention is held constant (Snyder et al. 1998a). Cells with a particular movement preference (reach or saccade) showed greater activity if a plan was changed from the nonpreferred to the preferred movement (for the same target location), compared to simply reaffirming the preferred

plan. This result is reminiscent of proposals that the PPC plays a role in shifting attention (Steinmetz & Constantinidis 1995), but in this case it is the intended movement that shifts, and not the spatial locus of attention.

Default Plans

The experiments by Snyder et al. (1997) were not the first to attempt to separate attention from intended movement activity. Bushnell and colleagues (1981) trained animals to either reach or saccade to a target while recording from PPC neurons. They reasoned that if the PPC was involved in attention then they should see the same level of activity regardless of the motor output, and this was what they reported. However, they recorded from only nine cells, and inspection of their Figure 1 suggests that the animal may have looked to the stimulus after the reach. Thus the animal may have been planning an eye movement as well as an arm movement during the task.

This potential problem of covert planning of eye movements is a general problem for experiments examining attention to targets placed away from the fixation point. While the formation of covert plans is unlikely to be critical for studies of attention in the ventral visual pathway, which current evidence suggests is largely involved in visual recognition, it is certainly a problem when studying the dorsal pathway, which is involved in movement planning. The issue of covert planning was directly addressed in Snyder et al. (1997). In the population of cells from which we recorded, 68% were significantly modulated in the delay period by one movement plan (reach or saccade) but not the other. Interestingly, even during the cue period 44% showed this specificity. We reasoned that the remaining cells showing significant activity for both movement plans might reflect covert plans for movement, since it is very natural to look to where you reach. To control for this possibility, we had the animals also perform a "dissociation" task in which they simultaneously planned an eye and an arm movement in different directions, with one movement into the response field and the other outside.

Figure 2 shows an example of a neuron that had activity for both eye and arm movements in the single-movement task. In the top row of histograms, the

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Figure 2 A posterior parietal cortex neuron whose motor specificity was revealed by a dissociation task. In saccade (*top*) and reach (*middle*) tasks, delay period activity was greater before movements in the preferred direction (*left*) compared to the null direction (*right*). Thus, in single-movement tasks, this neuron appeared to code remembered target location independent of movement intent. However, firing was vigorous in the delay period preceding a reach in the preferred direction when this reach was combined with a saccade in the null direction (*bottom left*), but firing was nearly absent before a saccade in the preferred direction combined with a null reach. Thus, when both a reach and a saccade were planned, delay-period activity reflected the intended reach and not the intended saccade. Panel formats similar to Figure 1 except that every other action potential is shown in the rasters. (Modified from Snyder et al. 1997.)

monkey performed only saccades, making eye movements into the response field (left histogram) or in the opposite direction (right histogram). In the middle row, the animal made reaches instead of saccades, and a similar level of activity is seen when the animal reaches into the response field. The bottom row of histograms shows activity from the same neuron while the animal was performing the dissociation


Preferred direction   Null direction
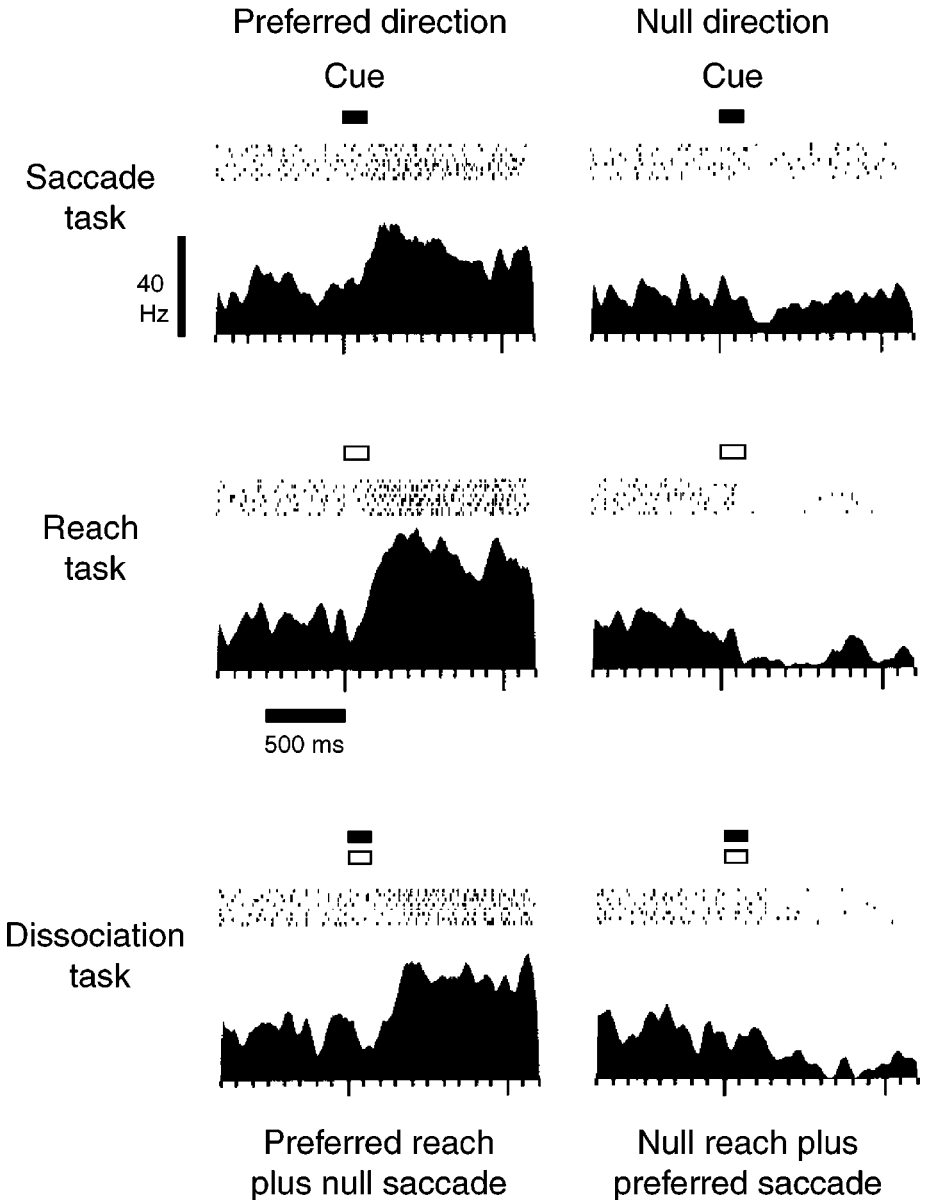
task. In the histogram on the left, the animal was simultaneously planning an arm movement into the response field and an eye movement out of the response field. In this case the cell was very active. In the histogram on the right, the animal was planning an eye movement into the response field, but an arm movement out of the field. Although this is the same eye movement plan that evoked activity in the single-movement case, now there is no activity or even a slight suppression. The pattern of activity of this neuron can be explained if the animal is forming a covert plan in the single-movement cases, in this example a covert arm movement plan. Of the neurons in the population, 62% that were not specific for single movements were specific in the dissociation task, bringing to 84% the number of cells that showed movement planning specificity in the delay period. Interestingly, more cells also revealed specificity for the cue response in the dissociation task, with a total of 45% being specific for reaches and 62% for saccades.

Covert planning may explain activity that is seen in go/no-go tasks. In these tasks a stimulus appears in the response field and the animal is later cued whether to make a movement to it or not. Activity in area 5 for reaches (Kalaska & Crammond 1995), and in LIP for saccades (Pare & Wurtz 1997) continues when the animal is cued not to move. This result is not consistent with attention or intention activity, since the target is no longer important to the animal's behavior (Pare & Wurtz 1997). However, it is consistent with a covert or default plan, which remains if no new movement plans are being formed. Evidence for this alternative explanation comes from experiments in which the plan is cancelled, and a new movement plan is put in place (Bracewell et al. 1996). An example is shown in Figure 3*a* and 3*b*, in which the monkey changed the movement plan three times before a

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Figure 3   Responses of PPC neurons when movement plans are changed. (*a*) Activity of an LIP neuron when saccades are planned into, out of, and then into the receptive field. The long horizontal bar indicates the onset and offset of a visual fixation point. Short horizontal bars represent the timings of three successive target presentations. Spike rasters show every action potential recorded in a given trial. Spike-density histograms were constructed using 50 ms binwidths. Thin horizontal lines below each histogram represent the animal's vertical eye position. Importantly, no saccades were initiated until after the fixation point was extinguished; thus changes in activity during the time of fixation correspond to changes in the animal's plans or intentions. (Modified from Bracewell et al. 1996). (*b*) Activity of the same neuron when saccades are planned out of, into, and then out of the cell's receptive field. (Modified from Bracewell et al. 1996). (*c*) Activity of a neuron in the parietal reach region when the type of movement plan, but not its direction, is changed. 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 changed to a reach activity increased (R2). Each ribbon represents the mean response of 8–12 trials +/−1 SE. Data were smoothed with a 121-point digital low-pass filter, transition band 20–32 Hz. Dashed rectangles indicate the timings target flashes. (Modified from Snyder et al. 1998a.)
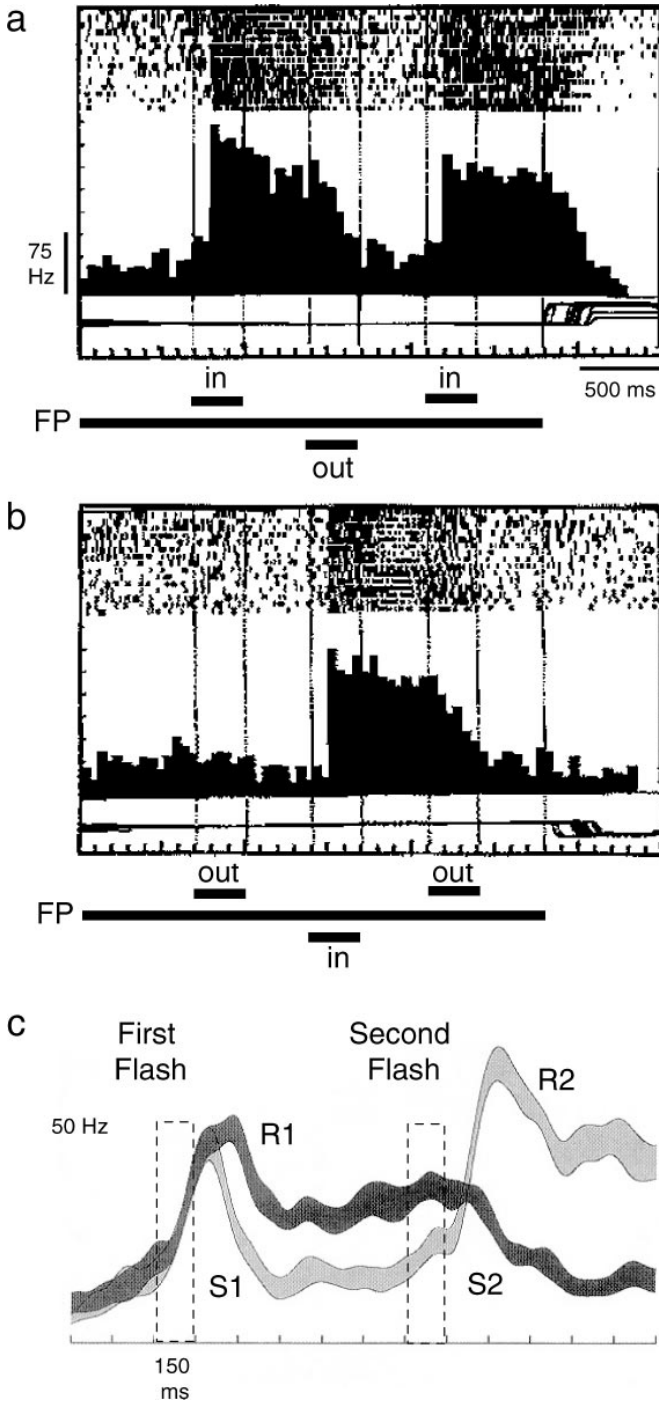
saccade, alternating between planning into, out of, and into the response field (*a*), or out, in, and out (*b*). A similar result is found even when the type of movement plan is changed, but not the direction (Snyder et al. 1998a). In Figure 3*c*, the dark histogram shows activity for a reach-specific neuron when the first cue presented in the response field instructs a reach (R1), and the second stimulus appears at the same location instructing a change in plan to a saccade (S2). Note that although no movement is made during the time shown in the histogram, the activity turns off when the animal changes to the nonpreferred plan for a movement to the same location. The lighter histogram shows activity for the same cell when the monkey plans a saccade first (S1), and then changes the plan to a reach (R2). Again the activity is consistent with the cell's activity expressing the intent of the animal, with baseline activity after the cue transient when the animal is planning a saccade, and high activity during the delay when he changes his plan to a reach. Taken together, the data from various labs suggest that default plans are formed in parietal areas to stimuli of behavioral significance in the case of no alternative plans, but are erased if alternative plans are formed.

Dynamic Evolution of Intention-Related Activity

Several studies point to a dynamic evolution in the relation of PPC activity to task requirements, changing from sensory to cognitive to motor as the demands of the task change. For instance, we recently examined the activity of PRR neurons when monkeys plan reaches to auditory versus visual targets in a memory-reach task. We found that at cue onset activity for visually cued trials carried more information about spatial location than activity for auditory cued trials. However, as the trials progressed and the animal was preparing a movement, the amount of spatial location information increased for the auditory cued trials so that by the time of the reach movement, it was not significantly different from the visually cued trials (Y. C. Cohen & R. A. Andersen, unpublished observations).

In another study, we trained animals to make saccades to a specific location cued on an object, but after the cue and before the saccade the object was rotated. Early in the task area LIP cells carried information about the location of the cue and the orientation of the object, both pieces of information being important for solving the task. However, near the time of the eye movement many of these same neurons predominately coded just the direction of the intended movement (Breznen et al. 1999).

Platt & Glimcher (1999) showed in a delayed eye movement task that the early activity of LIP neurons varied as a function of the expected probability that a stimulus was a target for a saccade, as well as the amount of reward previously associated with the target. However, during later periods of the trial the cells coded only the direction of the planned eye movement. A similar evolution has been shown in LIP and dorsal prefrontal cortex in eye movement tasks instructed by motion signals. The strength of the motion signal is an important determinant of activity in the beginning of the trial, but at the end of the trial the activity codes the decision or

movement plan of the animal (Leon & Shadlen 1999, Shadlen & Newsome 1996). These studies emphasize the fact that the circuits involved in sensory-motor transformations are distributed in nature, involving parietal, frontal, and prefrontal areas (Chaffee & Goldman-Rakic 1998). Moreover, activity in these circuits can evolve dynamically to reflect sensory, cognitive, and movement components of behavior.

Intentional Maps

The above studies point to a map of intentions within the PPC (Figure 4). Area LIP is more specialized for saccade planning, and area MIP for reaching. Work by other investigators implicates areas 5, PO, 7m, and PEc as additional reaching-related regions within the posterior parietal cortex (Battaglia-Mayer et al. 2000, Ferraina et al. 2001, Ferraina et al. 1997, Kalaska 1996). Recent studies by Sakata and colleagues (1995, 1997) point to the anterior intraparietal area (AIP) as specialized for grasping. Cells in this area respond to the shapes of objects and the configuration of the hand for grasping the objects. Reversible inactivations of AIP produce deficits in shaping the hand prior to grasping in monkeys. This deficit is reminiscent of problems in shaping the hands prior to grasping found in humans with parietal lobe damage (Perenin & Vighetto 1988). The medial superior temporal area (MST)
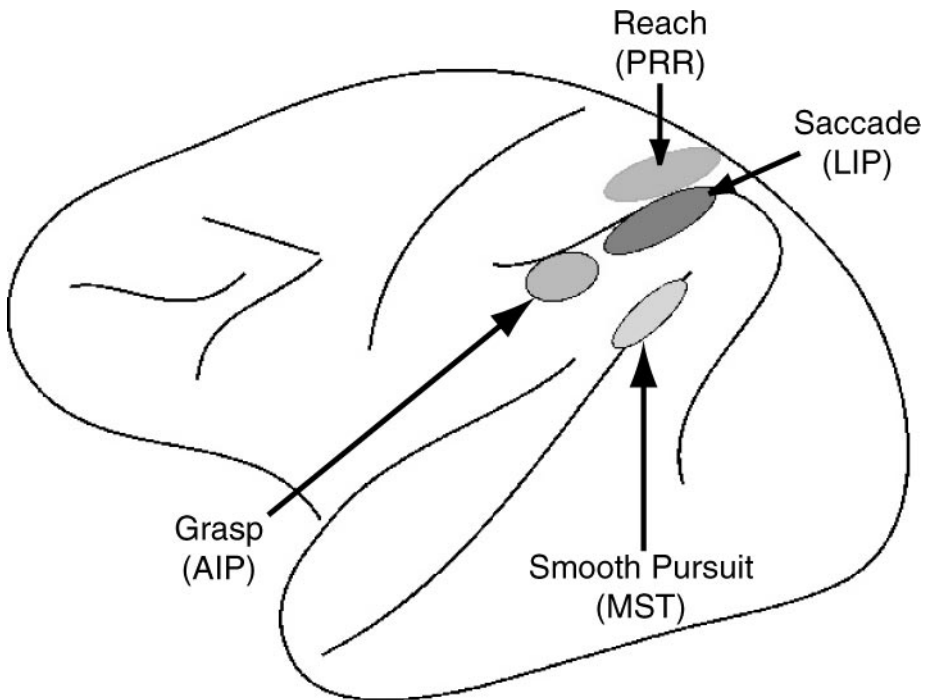
Figure 4   Anatomical map of intentions in the PPC.

appears to play a specialized role in smooth-pursuit eye movements. Cells in this area are active for pursuit, even during brief periods when the pursuit target is extinguished (Newsome et al. 1988). Inactivations of this area produce pursuit deficits that are not a result of sensory deficits (Dursteler & Wurtz 1988).

Experiments using fMRI in humans are consistent with the monkey results. Rushworth and colleagues (2001b) found that peripheral attention tasks activated the lateral bank of the intraparietal sulcus, whereas planning manual movements activated the medial bank. They concluded that their results were consistent with the monkey studies, with the medial bank specialized for manual movements and the lateral bank for attention and eye movements. A similar result has recently been reported by Connolly et al. (2000) using event-related fMRI and an eye and hand movement task similar to the one employed by Snyder et al. (1997). An area specialized for grasping has also been identified in the anterior aspect of the intraparietal sulcus in humans (Binkofski et al. 1998). This area may be homologous to monkey AIP.

Multisensory Integration and Coordinate Transformations

Producing a movement in response to a sensory stimulus requires that a host of problems be solved. From the sensory side, different sensory modalities are coded in different reference frames, vision in retinal or eye-centered coordinates, sound in head-centered coordinates, and touch in body-centered coordinates. These different coordinate frames need to be resolved in some way, since a particular movement might need to be directed to a visual, auditory, or somatosensory stimulus or any combination of these. From the motor side, the locations of these stimuli must ultimately be transformed into the natural coordinates of the muscles in order to make movements.

Lesions to the PPC can produce optic ataxia, where patients mislocalize stimuli to which they are reaching. These mislocalizations are apparent in all three dimensions. Since these effects are often present with no primary sensory or motor defects, they suggest that the PPC is important for multisensory integration as well as for the coordinate transformations required for making sensory-guided movements. In this section, we discuss electrophysiological experiments supporting this view. In particular, we provide evidence that spatial locations are represented in a common coordinate frame in at least some parts of the PPC, independent of sensory input or motor output.

AREA LIP: SACCADE PLANNING IN EYE-CENTERED COORDINATES We can easily make eye movements to visual or auditory targets. If area LIP is involved in making eye movements, then cells in this area should respond when an animal is planning an eye movement, regardless of the sensory modality of the stimulus. Recently we have found this to be the case (Grunewald et al. 1999, Linden et al. 1999, Mazzoni et al. 1996b). However, this observation raises the question, do these two modalities share a common reference frame, and if so, what is it? Cells in the intermediate

layers of the SC use a common, eye-position-dependent reference frame for representing saccades to visual, auditory, or somatosensory stimuli (Groh & Sparks 1996a, Groh & Sparks 1996b, Jay & Sparks 1987a, Jay & Sparks 1987b). This is not surprising given that the SC is near the final motor output stage for saccades and that motor error is expressed in eye-centered coordinates. However, area LIP is intermediate between sensory and motor areas; thus it is not immediately apparent what reference frame should be used to represent visual and auditory targets in this region.

In experiments in which monkeys made saccades to auditory targets, we found that a majority of the neurons coded these targets in eye-centered coordinates, although some also coded auditory targets in head-centered coordinates, or in a reference frame intermediate between the eye and head reference frames (Stricanne et al. 1996). Moreover, many of the response fields of LIP neurons were gain modulated by eye position. These data suggest that area LIP may be one of the sites involved in the transformation of auditory signals from head- to eye-centered coordinates. Recent experiments examining cells in the temporo-parietal cortex (TpT) (Wu & Andersen 2001), an auditory association area that projects into the PPC (Pandya & Kuypers 1969), and the inferior colliculus (Groh et al. 2001), indicate that cells antecedent to LIP code auditory locations in head-centered coordinates, with many neurons also gain modulated by eye position. These results support a model in which head-centered auditory signals are gain modulated by eye position and are then read out at subsequent levels in eye-centered coordinates (Xing & Andersen 2000b).

PRR: REACH PLANNING IN EYE-CENTERED COORDINATES   The LIP results suggest that this area encodes sensory stimuli as motor error for saccades. If this is the case, then one might predict that PRR would code sensory stimuli as motor error as well, i.e., in limb coordinates. We tested this prediction by training monkeys to reach to targets from two different initial arm positions while fixating their gaze in two different directions. As illustrated for one PRR neuron in Figure 5, the response field did not vary with changes in limb position (*a,b*), but shifted with gaze direction (*c,d*). This result indicates that PRR codes limb movements in eye-centered coordinates. This result, as well as those obtained in LIP, indicates that the PPC is capable of encoding intended movements in eye-centered coordinates independent of the type of movement to be made, i.e., saccades (LIP) and reaches (PRR) (see Figure 6).

The finding that area LIP encodes intended saccades in eye-centered coordinates for both visual and auditory stimuli, as well as the finding that area PRR encodes reaches in eye-centered coordinates, led us to an unusual prediction: that PRR would code reaches to auditory stimuli in eye-centered coordinates. This prediction is based on the assumption that the PPC may use a common reference frame for movement planning, independent of sensory input or motor output. Such a result would be quite surprising since sounds, which are initially coded in head-centered coordinates, could simply be converted to body- and then limb-centered

coordinates—a transformation to eye-centered coordinates is not required. In a study in which monkeys planned reaches to sounds in complete darkness, we found that this prediction was correct. Under these conditions, many cells in PRR encoded the intended movement in eye-centered coordinates (Cohen & Andersen 2000).

EYE-CENTERED CODING IN OTHER AREAS   Recent stimulation studies suggest that the SC, rather than coding desired gaze displacement or gaze direction in space, encodes the desired gaze direction in retinal coordinates (Klier et al. 2001). Electrophysiological studies of the SC have provided evidence for an eye-centered coding of limb movements in this structure as well (Stuphorn et al. 2000). The ventral premotor cortex also appears to contain neurons that code the location of reach targets in eye-centered coordinates (Mushiake et al. 1997), though these cells may coexist with others having more arm-centered properties (Graziano et al. 1994, 1997). These results, as well as those obtained in the PPC, support the existence of a distributed network devoted to eye-hand coordination that uses a common eye-centered reference frame for representing the spatial aspects of eye and arm movements (Figure 6).

COMPENSATION FOR EYE MOVEMENTS   If saccade and reach plans are coded in eye-centered coordinates, then problems can arise in situations where a movement plan is formed and an intervening saccade is made before the movement is executed. The problem is particularly acute in cases of movements planned to remembered locations in the dark. Mays & Sparks (1980) found that under these circumstances, activity shifts within the eye movement map of the SC to compensate for the intervening saccade and to still code the correct motor vector. Gnadt & Andersen (1988) reported a similar result in area LIP. Duhamel et al. (1992) extended these results by showing that it was not necessary to make an eye movement for this updating to take place. They interpreted this updated activity as sensory and a mechanism for maintaining perceptual stability across eye movements. The results of Snyder et al. (1997, 1998a) provide an alternative explanation: that this activity reflects a default plan for an eye movement. Whether this shift also accounts for perceptual stability remains a possibility and requires additional investigation.

Accounting for eye movements is also a problem when reach plans are coded in eye-centered coordinates. Imagine that an animal plans an arm movement in eye-centered coordinates to the remembered location of a stimulus in the dark and then makes an intervening eye movement before the arm movement takes place. If the reach plan is not adjusted to take into account the retinal position of the stimulus after the eye movement, then areas downstream of PRR will use the previous retinal position of the stimulus to calculate the motor error. This will result in an error corresponding to the size and direction of the intervening saccade.

We directly tested the effect of intervening saccades on intended reach activity in PRR. Figure 5e–g shows the design of the experiment and results from one cell. When the flash occurred outside the response field there was no response (e), and when it fell within the response field there was robust

planning activity (*f*). Note that the histograms demonstrate planning activity; the actual arm movement occurs at a time later than that shown. In (*g*), the task began with the same configuration of eye, hand, and stimulus as in (*e*). However, after the stimulus was extinguished, the animal was instructed to make a saccade to a new location on the board, bringing the response field over the location on the board where the animal was planning the reach. The activity shifted in PRR such that the cell was now active, coding the correct location of the planned reach in eye coordinates even though the reach cue never appeared in the response field. Thus the cell compensated for the saccade to maintain the correct coding of the reach target in eye coordinates. All 34 PRR cells tested with this paradigm showed such compensation for saccades. A remapping of reach plans in eye coordinates has been demonstrated in psychophysical experiments in humans (Henriques et al. 1998), consistent with this physiological finding.

Another possible example of this type of compensation for eye movements, which must still be experimentally verified, is the compensation for smooth-pursuit eye movements that must occur for self-motion perception. During forward loco-motion, self-motion perception is estimated from the focus of expansion of the visual field. However, when subjects make smooth eye movements during forward locomotion, as would occur when tracking an object on the ground, these eye movements introduce an additional, laminar motion on the retinas that disrupts the focus of expansion, generally shifting it in the direction of the eye movement. Cells in the dorsal subdivision of the medial superior temporal area (MSTd) are thought to play a role in self-motion perception because they are sensitive to optic flow stimuli and because they are tuned to the spatial location of the focus of expansion (Duffy & Wurtz 1995). In experiments from our laboratory, we found that these focus tuning curves shift to compensate for smooth-pursuit gaze movements. This compensation appears to depend on both efference copies of commands to move the eye or head and the visual information in the optic flow pattern (Bradley et al. 1996, Shenoy et al. 1999a). To guide locomotion, this signal would eventually need to be coded in body- or world-centered coordinates; however, it is currently not known in what reference frame MSTd neurons code focus-position signals. It would be consistent with the data from LIP and PRR if the MSTd cells compensated for the eye movements to maintain the correct heading direction in eye-centered coordinates.

GAIN FIELDS   The common representation of space in the PPC is embodied not only in eye-centered response fields, but also in the gain modulation of these fields by body-position signals. These gain field effects are found throughout the PPC and include modulation of retinotopic fields by eye-, head-, body-, and limb-position signals (Andersen et al. 1993). Computational studies have shown that these gain effects can be the mechanism for transforming between coordinate frames (Salinas & Abbott 1995, Zipser & Andersen 1988). Moreover, groups of neurons with retinal response fields, modulated by various body part–position signals, can conceivably be read out in multiple frames of reference (Pouget &

Snyder 2000, Xing & Andersen 2000b) as would be needed to direct movements of the eyes, head, or hand. Thus the representation of space in the PPC is distributed and is comprised of eye-centered response fields with gain modulation.

A potential problem with this type of representation is the "curse of dimensionality." For example, if it takes 10 cells to tile each dimension in visual space, and 10 for each dimension of eye position, head position, etc., the number of cells required to represent all possible combinations of such signals quickly exceeds the number of neurons in the brain. One method the PPC employs to avoid this combinatorial explosion is to code only a limited number of variables in each of its subdivisions (Snyder et al. 1998b). We have found that area LIP and area 7a both carry information about head position that is used to gain modulate the cells in this area. In area LIP this information is derived from neck proprioceptive signals indicating the orientation of the head on the body, whereas in area 7a the information is derived from vestibular signals and indicates the orientation of the head in the world. Thus, activity in LIP can be read out in body-centered coordinates, while activity in 7a can be read out in world-centered coordinates. One possible reason for this paucity of dimensionality is that area LIP may be concerned primarily with representing space for gaze shifts and eye-head coordination, whereas area 7a may be more related to representing space for navigation. In other words, these areas and possibly other cortical areas may only represent as many dimensions as are needed for the particular functions they perform. Knowledge of those dimensions may provide clues to the function of a particular area.

GAIN FIELDS AND REMAPPING   As mentioned above, eye movements are compensated for within PPC representations by shifting activity within eye-centered maps. Such a remapping of activity is necessary if coordinate transformations are to be accurately achieved using a gain mechanism. For instance, if the eyes move, the new location of a stimulus or planned movement must be adjusted in eye coordinates to correctly read out the head-centered location of the target. An important question is how this remapping is achieved. It could be accomplished using an eye displacement signal, or it could be accomplished using an eye position signal. Both eye displacement and eye position–related signals are found in the PPC (Mountcastle et al. 1975).

The experimental protocol typically used for examining remapping is the "double saccade" paradigm, in which an animal remembers two sequentially flashed targets and makes eye movements to the remembered locations of the targets in the order of their appearance. Activity in LIP appears for the next impending movement and disappears for the previous movement (Gnadt & Andersen 1988, Mazzoni et al. 1996a). More importantly, the activity for the second saccade specifies the direction and amplitude of the planned saccade, not the location on the retina in which the second flash occurred prior to the first eye movement. This compensation requires taking into account either the eye displacement for the first saccade or the new eye position after the first saccade. Patients with PPC lesions performing double saccades can make the first eye movement into the unhealthy

visual field, but are not able to generate an accurate second saccade (Heide et al. 1995). Although it has been argued that this proves that an eye-displacement signal mediates remapping, eye displacement and eye position are in fact confounded in this task. The deficit was seen when the displacement of the eyes was in the direction of the unhealthy field, but also when the eye position after the first movement was in the unhealthy field.

In other experiments, area LIP was reversibly inactivated in monkeys in experiments designed to directly examine whether eye-displacement or eye-position signals are used for remapping in double-saccade experiments (Li & Andersen 2001). Both initial eye position and the direction of eye movements were varied in individual trials in order to tease apart eye-position and eye-displacement contributions. It was found that the largest deficits were seen when the animal made the first eye movement into the unhealthy visual field, largely independent of the direction of the eye movement. This result suggests that eye-position signals play a large role in the compensation for intervening saccades.

A recent computational study illustrates that dynamic neural networks can be trained to perform the double saccade task using eye-position signals (Xing & Andersen 2000a). These networks show activity similar to that recorded from LIP when monkeys perform the same task. These include eye-centered response fields that are gain modulated by eye position, and activity that shifts within an eye-centered map of visual space to correct for intervening saccades. Thus, the gain field mechanism can account for dynamic compensation for intervening eye movements in eye-centered coordinates.

GAIN FIELDS: OTHER USES   Since their discovery in areas of the PPC, gain effects have been identified throughout the brain. This suggests that multiplicative and additive interactions between different inputs to neurons may reflect a general method of neural computation. Although the role of gain fields in coordinate transformations has been highlighted in this review, gain fields appear to play a role in many other functions, including attention, navigation, decision making, and object recognition. Some examples are discussed briefly below (see also Salinas & Thier 2000).
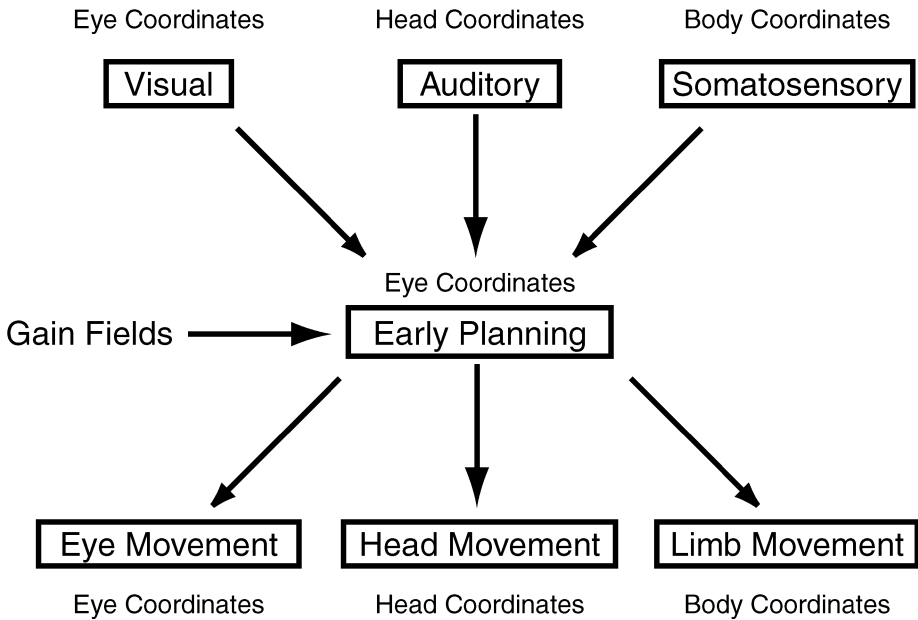
The direction of attention can modulate the activity of V4 neurons (McAdams & Maunsell 2000, Reynolds et al. 2000), and this effect has been proposed to play a role in the binding of features in objects (Salinas & Abbott 1997). In addition, although smooth pursuit shifts the focus tuning of many MSTd neurons, as mentioned above, other MSTd neurons do not shift their focus tuning but are gain modulated by the pursuit signal (Bradley et al. 1996, Shenoy et al. 1999a). This gain modulation is consistent with an intermediate step toward the production of shifting focus-tuning curves, and thus may play a role in the perception of self-motion for navigation. Monkeys and humans have been shown to choose between two targets for a reach depending on eye position, essentially choosing targets that tend to center the reach with respect to the head (Scherberger et al. 1999). Eye-position gain effects have been shown in PRR and may bias

the decision of animals to choose targets based on eye position (Scherberger & Andersen 2001).

We have recently trained monkeys to make object-based saccades by cueing a location on an object, extinguishing the object, and then presenting the object again at a different orientation. In this task, the animals must saccade to the previously cued location on the object to obtain their reward (Breznen et al. 1999). We find that area LIP does not code the cued location in an explicit object-centered reference frame in this task, even though it requires the animal to code the target in such a reference frame. Rather, cells in area LIP carry information about the cued location, movement vector, and orientation of the object, all in retinal coordinates. Some cells show a gain modulation of the cue or movement vector activity by object orientation. This result is surprising given the finding that lesions to the PPC in humans often produce deficits in object-centered coordinates (Arguin & Bub 1993, Driver & Mattingley 1998). However, computational studies show that it is not necessary to use cells with object-centered response fields to solve object-based tasks; rather, distributed coding using retinal response fields for target locations and object orientations, and gain modulations between the two, is sufficient (Pouget & Sejnowski 1997). This distributed representation can be used to form response fields in object-centered coordinates, as has been reported in the supplementary eye fields (SEF) (Olson 2001). However, the SEF results may also be explained as a result of gain modulation of retinal response fields by object position (Pouget & Sejnowski 1997), and more thorough mapping of the response fields will be required to distinguish between the two possibilities.

A COMMON DISTRIBUTED CODE FOR INTENDED MOVEMENTS IN AREAS LIP AND PRR   The above results, summarized in Figure 6, suggest that LIP and PRR use a common space representation in which response fields are represented in eye-centered coordinates. This representation exists independent of whether the targets are visual or auditory. Likewise, this representation is used regardless of whether the output is to move the limb or make an eye movement. This general scheme generated a nonintuitive, but correct, prediction that auditory targets for reach would be coded in eye-centered coordinates in PRR. Currently, we do not know if somatosensory stimuli, such as proprioceptive signals coding the position of the hand, are coded in eye coordinates in PRR and LIP. This would be an interesting question for future experimentation, and if true, would provide further evidence for the generality of this model. In both LIP and PRR, the eye-centered response fields are gain modulated by eye-, head-, and limb-position signals. This gain modulation may provide the mechanism for converting stimuli in various reference frames into eye-centered coordinates. Likewise, these gain modulations may allow other areas to read out signals from LIP and PRR in different coordinate frames, including eye-, head-, body-, and limb-centered coordinates.

Why use a common coordinate frame for PRR and LIP? One possibility is to facilitate hand-eye coordination. Presumably the orchestration of these movements would be facilitated if they used a common reference frame (Battaglia-Mayer et al. 2000). A second reason may be that vision is the most accurate spatial sense in

Eye Coordinates   Head Coordinates   Body Coordinates

| Visual | Auditory | Somatosensory |

Eye Coordinates

Gain Fields ⟶ Early Planning

| Eye Movement | Head Movement | Limb Movement |

Eye Coordinates   Head Coordinates   Body Coordinates

Figure 6   Theory of multisensory integration and coordinate transformations subserved by the PPC.

primates. This dominance of vision may explain certain illusions, such as the ventriloquist effect, in which the spatial locations of sounds are referred to seen objects.

COORDINATE TRANSFORMATIONS FOR REACH—DIRECT TRANSFORMATION   To make visually guided reaching movements, the location of the target for the reach must be converted from eye- to limb-centered coordinates. There have been two general schemes for this transformation in the literature. One we refer to as the sequential method, shown in Figure 7*a* (Flanders et al. 1992; McIntyre et al. 1997, 1998). In this scheme, visual signals in retinal coordinates are combined with eye-position signals to represent targets in head-centered coordinates. Next, head position is combined with the representation of target location in head-centered coordinates to form a representation of the target in body-centered coordinates. Finally, the current location of the limb (in body-centered coordinates) is subtracted from the location of the target (in body-centered coordinates) to generate the motor vector, in limb-centered coordinates. There are two drawbacks to this method. One is that it requires a number of stages and separate computations, which would likely require a large number of neurons and cortical areas. The second is that, although there are some reports of cells in the PPC coding targets in head-centered coordinates (Duhamel et al. 1997, Galletti et al. 1993), the vast majority of PPC cells code visual targets in eye-centered coordinates and not head- or body-centered coordinates.

A second scheme is referred to as the combinatorial method. As shown in Figure 7b, retinal target location, eye, head, and limb position are all combined at once, and the target location in limb-centered coordinates is then read out from this representation (Battaglia-Mayer et al. 2000). As mentioned above, a drawback to this approach is the "curse of dimensionality."

A third scheme we refer to as the direct method. Figure 7c shows that this approach subtracts the current position of the hand (in eye coordinates) from the position of the target (in eye coordinates) to directly generate the motor vector in limb coordinates. An advantage of this approach over the sequential method is that it requires fewer computational stages. In addition the computation is restricted to only dimensions in eye coordinates and does not suffer the curse of dimensionality of the combinatorial approach.

Recently, we have provided evidence for the direct transformation scheme. Single cells in area 5, a somatomotor cortical area within the PPC, have been found to code target locations simultaneously in eye- and limb-centered coordinates (Buneo et al. 2002). This result suggests that the PPC transforms target locations directly between these two frames of reference. Moreover, cells in PRR code the target location in eye-centered coordinates, but the initial hand position introduces a gain on this response that is also eye centered. These two findings, taken together, suggest that a simple gain field mechanism underlies the transformation from eye- to limb-centered coordinates. A convergence of input from cells in PRR onto area 5 neurons can perform this transformation directly (see Figure 7d) without having to resort to intermediate coordinate frames or a large combination of retina-, eye-, head-, and limb-position signals.

Psychophysical evidence supporting a sequential scheme has been provided by Flanders et al. (1992), Henriques et al. (1998), and McIntyre et al. (1997, 1998). These results, as well as our own physiological studies supporting an alternative direct scheme, may reflect an underlying context dependence in the coordinate transformations that subserves visually guided reaching (Carrozzo et al. 1999). For example, direct transformations may be the preferred scheme when both target location and the current hand position are simultaneously visible, even for a brief instant. In contrast, a sequential scheme may be used when visual information about the current position of the hand is unavailable.

MOVEMENT DECISIONS

Experiments in LIP by Platt & Glimcher (1999) and by Shadlen and colleagues (Kim & Shadlen 1999, Shadlen & Newsome 1996) have found activity related to the decision of a monkey to make eye movements. Both the prior probability and amount of reward influence the effectiveness of visual stimuli in LIP, consistent with a role for this area in decision making. As monkeys accumulate sensory information to make a movement plan, activity increases for neurons in LIP and the prefrontal cortex (Kim & Shadlen 1999, Leon & Shadlen 1999, Shadlen & Newsome 1996). These results are consistent with these areas weighting decision variables for the purpose of planning eye movements (Gold & Shadlen 2001). The

fact that these effects appear in multiple brain areas suggests that decision making is a distributed function that includes the PPC.

ATTENTION

The PPC has been classically thought to play a central, perhaps controlling role in attention. Strong evidence for this idea is the finding of neglect, an inability to attend to the contralateral visual field, after PPC lesions in humans (Critchley 1953). However, many of the processes involved in visual-motor transformations, for example the shaping of the hand for grasping, appear to operate unconsciously (Goodale & Milner 1992). In fact, lesions to the PPC in monkeys produce visual-motor deficits and not neglect (Faugier-Grimaud et al. 1978, Lamotte & Acuna 1978). Rather, it has been reported that lesions to the superior temporal gyrus produce neglect similar to that found in humans (Watson et al. 1994). Interestingly, a recent report by Karnath and colleagues (2001) suggests that the superior temporal gyrus damage may also be the source of neglect seen in humans. Thus, the locus of cortical lesions that produce neglect is still an open question that will likely be resolved with further research.

Although there have been several studies reporting attentional effects on neural activity in the PPC, these experiments have been performed in conjunction with eye or limb movements, or in peripheral attention paradigms where animals are likely to form covert plans for eye movements. As yet no experiments have been performed similar to those of Snyder et al. (1997, 1998a). In those experiments, intention was isolated from attentional effects; similar experimental designs are needed to isolate attentional effects from intentional effects.

It has been argued that the lower degree of activation of LIP neurons when monkeys reach rather than saccade to targets is due to less attention being required for reaching (Colby & Goldberg 1999). This reasoning would predict less activity in PRR as well, but in fact the reverse is true. Figure 8 shows the population activity from one monkey for recordings obtained in LIP and PRR. When this monkey planned, a saccade activity was high in LIP and low in PRR. On the other hand, when reaches were planned the reverse was true. This figure also shows that when covert planning was controlled in dual-movement trials the separation for saccades and reaches was even greater. This double dissociation between saccades and reaches for LIP and PRR shows that the effects are due to planning, and not a general reduction in attention when the animal reaches.

In a recent study, Powell & Goldberg (2000) flashed stimuli around the time of eye movements and found responses for LIP neurons even while the animals were planning eye movements outside of the cells' response fields. They argued that this demonstrated that LIP is more involved in registering the salience of visual stimuli than in planning eye movements. This interpretation is at odds with that of Mazzoni et al. (1996a), who showed that, when monkeys were planning eye movements outside of the response field of LIP neurons, a flash in the center of their response field produced only a very brief transient before the activity was suppressed. A closer inspection of the data in Powell & Goldberg shows
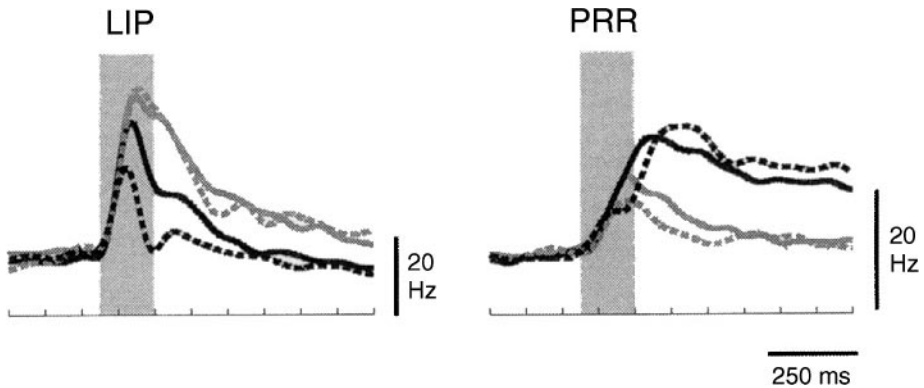
Figure 8   Population response from one monkey for areas LIP (*left*) and PRR (*right*). Cells had significant activity during the delay period of either the reach or saccade task of Snyder et al. (1997). Solid gray traces represent the average activity of the population of cells for saccades into the response field. Solid black traces represent activity for reaches into the response field. Dashed lines represent activity in the dual-movement task, with gray traces representing saccades into the response field and black traces representing reaches. Histograms were smoothed with a 181-point digital low-pass filter with a –3 dB point at 9 Hz. (From Snyder et al. 2000.)

a similar effect, with activity dying out prior to and during the eye movement. A similar sensory transient can be seen when a reach target is flashed within an LIP response field, which quickly dies away in this case hundreds of msec before the reach movement (see Figure 1*b*, right histogram). Interestingly, units in simulated networks programmed to hold a movement plan for one location while a distractor stimulus is briefly flashed at another location [conditions similar to the experiment of Powell & Goldberg (2000)] also exhibit input transients (Xing & Andersen 2000a). However, lateral inhibitory connections in these networks quickly suppressed the activity due to the distractor, similar to the suppression seen in LIP experiments.

In conclusion, it is likely that pure attentional effects will be found in the PPC. However, because this area is specialized for sensory-motor integration, there is the additional challenge of designing paradigms that rule out movement planning as a source of activity. This concern is less problematic in areas of the visual cortex that are involved in recognition, where there is ample evidence of attentional effects. Attentional effects in PPC may be general, since attention-related activity has been reported throughout the cerebral cortex. Thus attention effects in PPC would be related to planning movements, much like attention effects in inferotemporal cortex would be related to visual recognition. Interestingly, recent studies suggest PPC and prefrontal structures may regulate spatial aspects of attention in the ventral, recognition pathway (Kastner & Ungerleider 2000). Whether PPC is specialized for attention and is the controller for attention throughout cortex is an important question.

LEARNING AND ADAPTATION

Like attention, learning is a distributed function and like atttentional effects, learning effects in the PPC tend to be most apparent in the context of sensory-motor operations, for example prism adaptation. As first demonstrated by Held & Hein (1963), when human subjects reach to visual targets while wearing displacing prisms, they initially miss-reach in the direction of target displacement but gradually recover and reach correctly if provided with appropriate feedback about their errors. Using positron emission tomography (PET) to monitor changes in cerebral blood flow, Clower and colleagues (1996) showed that the prism adaptation process results in selective activation of the PPC contralateral to the reaching arm, when confounding sensory, motor, and cognitive effects are ruled out. Similarly, Rosetti and colleagues (1998) found that hemispatial neglect resulting from damage to the right hemisphere can be at least partially ameliorated by first having affected patients make reaching movements in the presence of a prismatic shift, then removing the prisms. They interpreted these effects as resulting from the stimulation of neural structures responsible for sensorimotor transformations, including the PPC as well as the cerebellum. A recent electrophysiological study employing a prism adaptation paradigm suggests that the ventral premotor cortex plays a role in this process as well (Kurata & Hoshi 1999).

An example of the effects of learning in the PPC was revealed in a recent electrophysiological study of LIP (Grunewald et al. 1999). The responses of LIP neurons to auditory stimuli in a passive fixation task were examined before and after animals were trained to make saccades to auditory targets. Before such training, the number of cells responding to auditory stimuli in LIP was statistically insignificant. After training, however, 12% showed significant responses to auditory stimuli. This indicates that at least some LIP neurons become active for auditory stimuli only after an animal has learned that these stimuli are important for oculomotor behavior. As with the learning effects discussed above, effects of this nature have been reported in other areas of cortex, e.g., area 3a for tactile discrimination (Recanzone et al. 1992), premotor cortex for arbitrary associations (Mitz et al. 1991), and the frontal eye fields (FEF) for visual search training (Bichot et al. 1996), highlighting the distributed nature of learning in cortex.

READING OUT INTENTIONS—THE PPC AND NEURAL PROSTHETICS

The experimental results reviewed above indicate that activity related to an animal's intentions to make reaches or saccades is strong and robust in the PPC. These experiments are typical of neurophysiological experiments in demonstrating correlations between behaviors or perception and neural activity. It would be powerful to be able to test these proposed linkages more directly. One method to achieve a more direct demonstration of intention coding is to perform experiments that close the loop. This type of experiment is demonstrated in Figure 9.
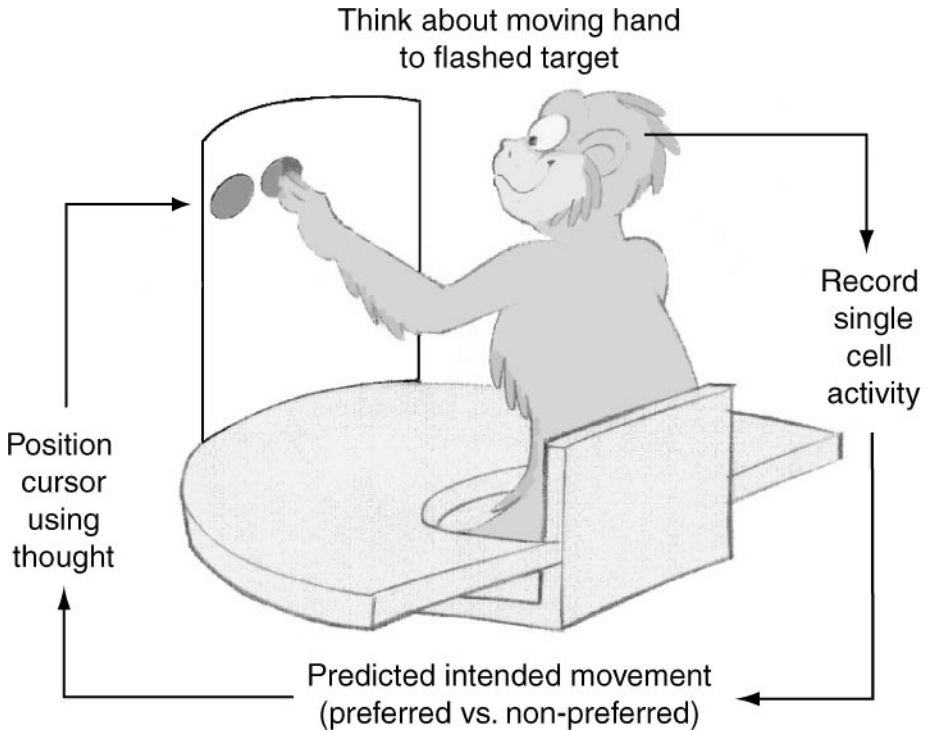
Figure 9 Schematic of an experiment in "closing the loop." In this experiment, the activity of a single-PRR neuron is first isolated and a database of the neuron's responses for reaches in the preferred and nonpreferred direction is constructed. In the relevant trials, the animal fixates and touches a central cursor on a display screen and a target is then presented either in the preferred or nonpreferred direction of the cell. Based on the response of the neuron for this one trial, and the statistics of the previously constructed database, we then predict whether this animal is intending to reach in either the preferred or nonpreferred direction. Importantly, the animal never actually makes the intended movement on these trials. A cursor moves to the location predicted from the cell activity and the animal is rewarded if the prediction corresponds to the cued location.

Rather than simply recording the monkeys' reach intentions from PRR and then rewarding them for making a reach, we record their intentions and use them to move a cursor to the location on the display screen where we predict, based on the neural activity, that they are intending to reach. This cursor provides feedback to the animals, indicating where the reach is predicted to end up, based purely on the animals' thoughts, i.e., without the animals making any actual reaches.

In preliminary studies we have used PRR activity to predict one out of two possible reach directions in real time (D. Meeker, S. Cao, J. W. Burdick & R. A. Andersen, unpublished observations). In other words, the animals perform a

task in which they locate a cursor on the computer screen by using intended move-
ment activity without making an actual reach. In other studies, offline analysis of
single-cell recordings from PRR indicates that reliably predicting one out of eight
directions could require only a small number of simultaneously recorded neurons,
perhaps in the range of 10 to 15 (Meeker et al. 2001, Shenoy et al. 1999b).

The high-level planning activity observed in PRR could be used in the control of
a neural prosthetic for paralyzed patients. Patients with paralysis due to peripheral
neuropathies, trauma, and stroke can often still think about making movements but
cannot execute them. The idea of a cortical prosthetic is to record these intentions
to move, interpret the intentions using real-time decode algorithms running on
computers, and then convert these decoded intentions to control signals that can
operate external devices. These external devices could include stimulators imbed-
ded in the patient's muscles that would allow the patient to move his/her own body,
a robot limb, or a computer interface for communication.

Research on neural prosthetics is a burgeoning and young field. Several groups
are working toward using motor cortex for such a prosthesis (Chapin et al. 1999,
Isaacs et al. 2000, Wessberg et al. 2000, Kennedy et al. 2000, Maynard et al.
1999), which makes sense because it is the area of cortex closest to the motor
output. There may also be advantages for using higher, cognitive areas of the
sensory-motor system such as PRR for the control of prosthetics. Because this is
a field that is still at its infancy, it is not clear if one area is optimal for prosthetic
control. Moreover, because different areas of the sensory-motor pathway no doubt
provide different, useful information, it may turn out to be most optimal to develop
multiarea prosthetics that can read out and decode these different signals. Below
are listed some potential attributes of PRR for prosthetic control.

1.) Motor cortex is known to undergo degradation as a result of paralysis. For
instance with spinal cord lesions, cortico-spinal neurons are destroyed and
the somatosensory reafferent signals to this area of the cortex are also lost.
However, PRR may undergo less degradation after paralysis as it is more
closely tied to the visual system.

2.) Learning is an important aspect of neural prosthetic success. For instance,
cochlear prosthetics do not produce natural auditory sensations with elec-
trical stimulation, but patients learn to interpret these stimulus-induced per-
cepts, for instance in understanding speech. Implanted arrays of electrodes
in humans will likely only sample a part of the workspace of the subject.
Although other parts of space not well sampled can be inferred from the
activity of cells in sampled regions, the resolution cannot be as good as
would result from a more even sampling. Thus, neural plasticity would be
an important advantage for a cortical prosthetic and, as mentioned above,
there is evidence that the PPC does play a role in adjusting the registration
of sensory-motor representations for accurate behaviors.

3.) To successfully close the loop, patients require feedback to the cortex re-
garding the success of the movement. Whereas these feedback signals are
lost with paralysis in motor areas, they are largely intact in PRR, as the

reafference to this region is largely visual. Moreover, the evidence presented above, that the PPC performs early coordinate transformations required for reaching in retinal coordinates, suggests that vision can be used by the patients for correcting motor error computations.

4.) The fact that the intended movement signal is a high-level, cognitive signal may have advantages. For instance, if PRR is coding intentions in abstract or general terms, it may require fewer neurons to control devices that are dissimilar to the human limb. In addition, the fact that this planning activity can be sustained for long periods of time may help in the decoding of the movement plan by providing prolonged, stable signals related to the intentions of the patient.

5.) We have recently found that, during the delays when monkeys are planning a movement, there are broadband gamma oscillations in the local field potentials (LFPs) in both LIP and PRR. The LFPs in both areas are tuned to the direction of planned movements and change their strength with behavioral state, becoming much larger in amplitude when the animal plans a movement and rapidly decreasing during the movement execution. Although it is somewhat difficult to record single-cell activity over long periods of time with chronically implanted electrodes, LFPs are stable and relatively easy to record with chronic electrodes, since they reflect the activity of cortical columns rather than single cells. Thus, using LFPs in LIP and PRR may be an important breakthrough for obtaining long-term recordings with existing technology.

CONCLUSION

The PPC is important for sensory-motor integration, particularly the forming of intentions or high-level cognitive plans for movement. There is a map of intentions within the PPC, with subregions for saccades, reaching, and grasping. These regions appear to be specialized for multisensory integration and coordinate transformations. Within each subregion is a map of the working space. In PRR and LIP these maps are in eye-centered coordinates, regardless of sensory input or movement plan. Within these maps, activity is gain modulated by eye-, head-, and limb-position signals. This distributed, abstract representation is consistent with intentions in this area being high level and cognitive.

These ideas perhaps raise more questions than they answer. For instance, what other features of intended movements are coded in the activity of PPC neurons? Are the trajectories, distance of reaching, or the dynamics of the planned movement coded in PRR activity? Is the transition from a high-level, cognitive intention to the motor output of the cortex one of multiple stages and continual refinement of the plan, or is the intention to move converted to an executable plan in one step of convergence onto motor cortical areas? Are there additional cortical areas in PPC for intending other types of movement, such as leg movements and head movements?

There are a number of outstanding questions regarding the finding of a common coordinate frame for spatial location in LIP and PRR. For instance, do other parietal areas, such as the grasp area, also code in retinal coordinates with gain modulation by eye- and other body part–position signals? Are somatosensory signals also represented in eye coordinates in these areas? Does this common reference frame also support intended head movements? Are there tasks in which the intentions to move do not use this common, distributed reference frame? Experiments designed to answer these questions will help to determine how generally the concepts of cognitive intentions and common reference frames can be applied to the PPC.

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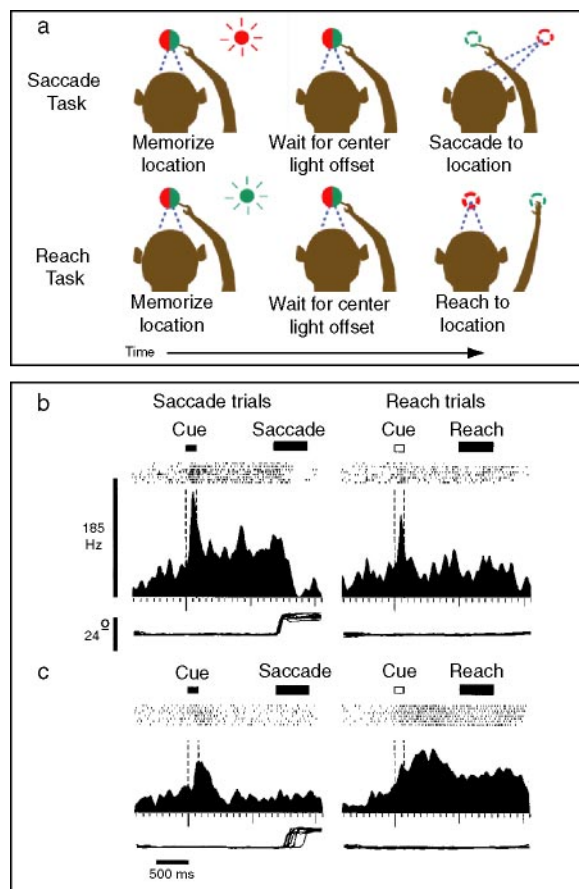
Figure 1 (*a*) Tasks used in Snyder et al. (1997) to separate the effects of spatial attention from those of intention. Animals made either a saccade (*top*) or a reach (*bottom*) to the remembered location of a flashed visual target (red flash: saccade, green flash: reach). Movements were made in complete darkness, after a delay period. (*b*) A lateral intraparietal area cell showing elevated delay period activity before a saccade (*left*) but not before a reach (*right*). *Vertical dashed lines* and *short horizontal bars* indicate the timing of target ("Cue") presentation (red flashes: filled bars, green flashes: open bars) and *long horizontal bars* indicate the timing of the motor response ("Saccade" or "Reach"). Each panel shows eight rasters of tick marks corresponding to every third action potential recorded during each of eight trials. Below each set of rasters is a spike density histogram representing the average rate of action potential firing over all trials (generated by convolution with a triangular kernel) that is aligned on cue presentation. *Thin horizontal lines* below each histogram represent the animal's vertical eye position on each trial. During the delay interval (150–600 msec after target extinction) firing depended specifically on motor intent. For illustration purposes, data for this cell were collected using a fixed delay interval. (*c*) A PRR cell showing reach rather than saccade specificity during the delay interval. (Modified from Snyder et al. 1997)
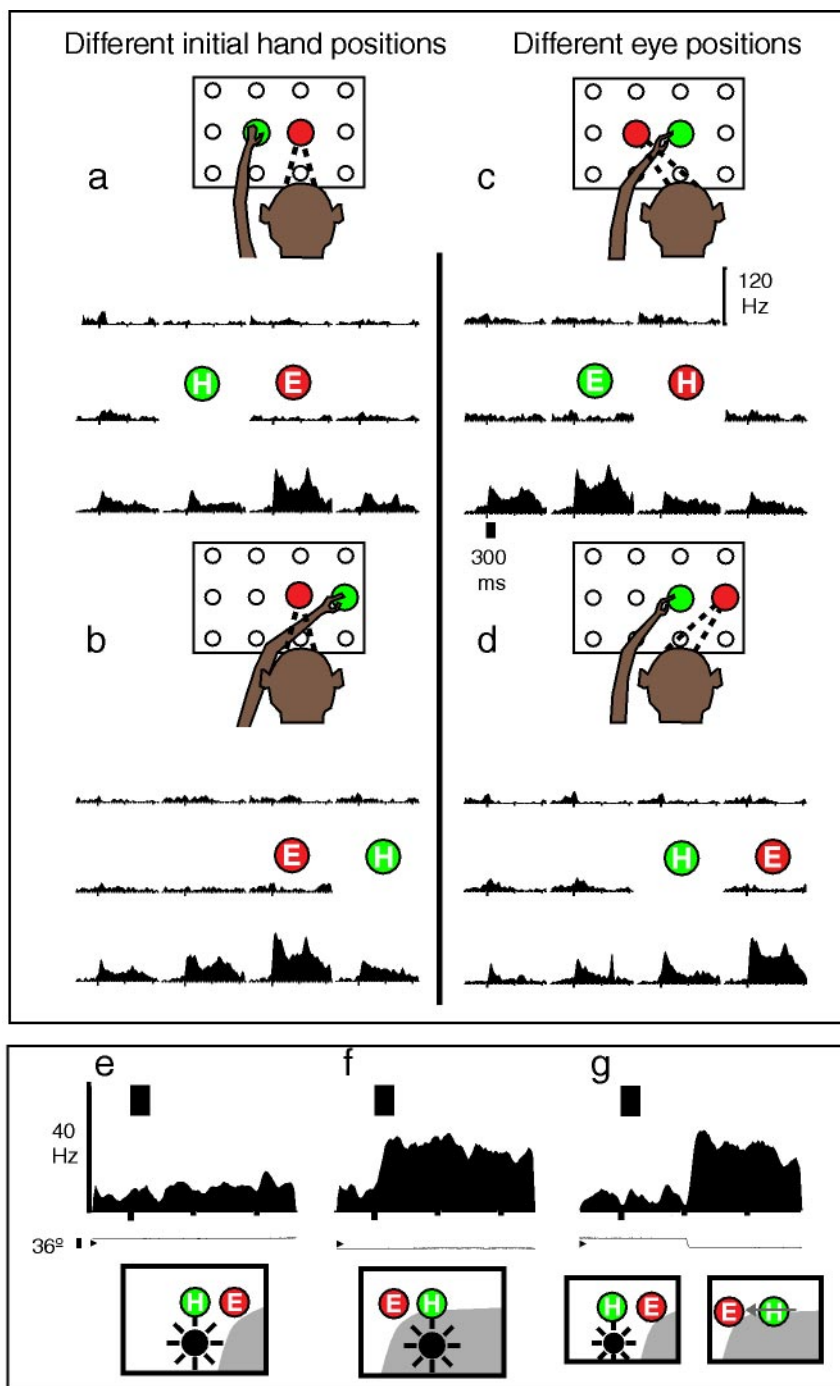
See legend on next page.

Figure 5 (See figure on previous page) (*a–d*) A PRR neuron that codes target locations in eye-centered coordinates. Icons depict the four possible behavioral conditions at the beginning of a trial; initial hand position and the point of visual fixation are represented by *green* and *red circles*, respectively. *Open circles* represent target locations on a vertically oriented board of push buttons. Below each icon, spike density histograms (aligned at cue onset and smoothed as in Figure 1) are plotted at positions corresponding to the target locations on the board (11 locations in *a*, *b*, and *d*; 10 locations in *c*). *Short horizontal bar* below the histograms in (*c*) represents the timing of the cue. The response field of this neuron did not vary with changes in limb position (*a*, *b*) but shifted with gaze direction (*c*, *d*). (Modified from Batista et al. 1999). (*e–g*) Activity of a PRR neuron in an intervening saccade experiment. Each spike density histogram shows the response of the cell for the experimental conditions illustrated in the corresponding icon (*below*). *Shaded region* represents the spatial extent of the cell's response field. (*e*) Activity when the target is presented outside of the response field. (*f*) Response when the target is in the response field. (*g*) Activity when an eye movement carries the reach goal into the neuron's response field. This cell compensated for the saccade to maintain the correct coding of the reach target in eye coordinates. The H and E in the icons below the histograms indicate the position of the hand and eye on the reach board, the *black target* indicates the location of a flashed reached target, and the *shaded area* indicates the spatial extent of the response field of a PRR neuron. The *squares* above the histograms show the time of the flashed target, and the *traces* below the histograms are the recorded eye positions. (Modified from Batista et al. 1999).
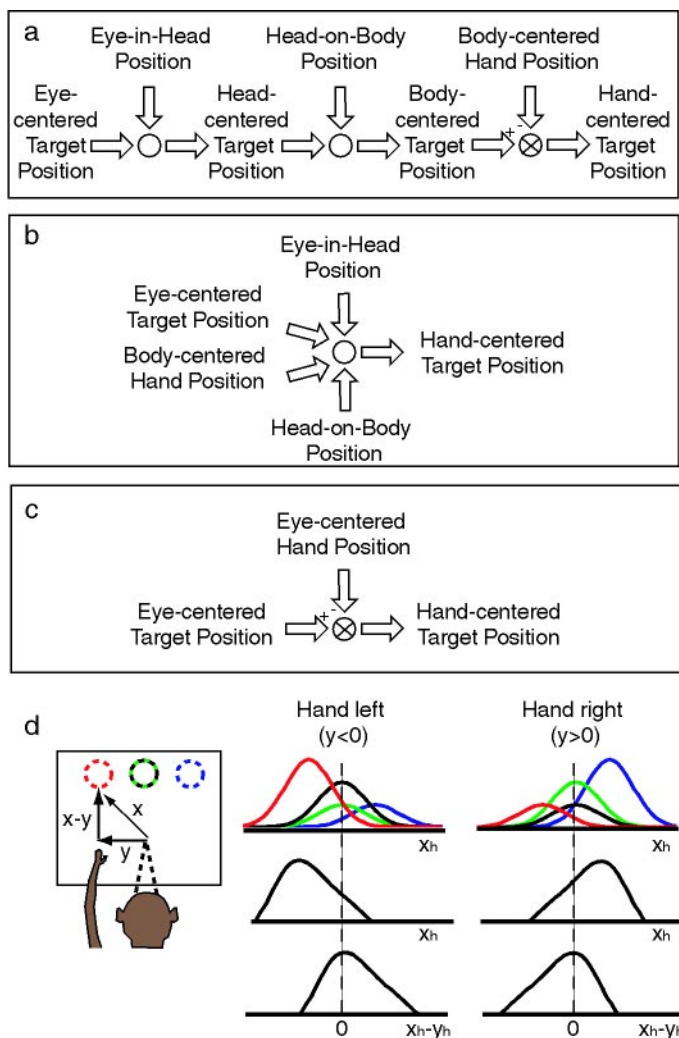
Figure 7 (*a–c*) Schemes for transforming target position from eye-centered to hand-centered coordinates. (*a*) Sequential method. (*b*) Combinatorial method. (*c*) Direct method. (*d*) Illustration showing how convergent input from neurons encoding target position (x) and initial hand position (y) in eye coordinates can drive downstream responses that encode target position in hand-centered coordinates (x-y), as in the direct method. *Top row of curves* represents the responses of four idealized neurons at two initial hand positions. *Middle* and *bottom rows* show the responses of a downstream neuron, derived as a weighted sum of the responses in the top row minus a constant (Salinas & Abbott 1995, Salinas & Thier 2000). When initial hand position varies, the peak response of the downstream neuron shifts in eye-centered coordinates (*middle row*), but remains fixed in hand-centered coordinates (*bottom row*). For simplicity, only the horizontal components of responses are shown.

CONTENTS

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