

34 Sensorimotor Transformations in the Posterior Parietal Cortex

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ABSTRACT The posterior parietal cortex (PPC) sits at the interface between sensory and motor areas and performs sensorimotor transformations. Current research is beginning to unravel the details of this transformation process. The first part of this chapter focuses on planning signals found in the PPC. Experiments show that the thought to reach can be read out from the parietal reach region of monkeys and used to control the position of a computer cursor without any reach movements being made by the monkeys. The second section reviews recent studies of coordinate transformations, which are an important aspect of sensorimotor transformations and involve the PPC.

Early studies of the posterior parietal cortex (PPC) identified movement-related and sensory-related signals (Mountcastle et al., 1975; Robinson, 1978; Andersen et al., 1987). Although debate continues over whether responses in PPC during sensory-guided movements are sensory or movement related, control experiments indicate that both signals are present (Andersen et al., 1987). Moreover, there seems to be a dynamic evolution of activity, with sensory responses and responses related to movement plans occurring early in delayed-response tasks and movement-related activity occurring later (Zhang and Barash, 2000; Cohen, Batista, and Andersen, 2002; Sabes, Breznen, and Andersen, 2002).

Although visual responses in the lateral intraparietal (LIP) area have been well documented for a number of years, their significance has recently been reinterpreted by Goldberg and colleagues (Powell and Goldberg, 2000; Goldberg et al., 2002; Bisley and Goldberg, 2003). They have argued that the existence of visual responses means that the signals in LIP cannot be related to movement plans. It has been further argued that the nature of responses in LIP would make it difficult for other parts of the brain to determine whether activity is related to sensory responses or movement plans. Finally, they proposed that the signals must therefore be signaling salience.

One problem with the interpretation of Goldberg and colleagues is that the two kinds of responses can be distinguished. In LIP, activity related to eye movements can be distinguished from activity related to arm movements, even when the visual stimuli instructing these different movement types are similar (Snyder et al., 1997, 2000). The same is true in the parietal reach region (PRR). In LIP, when monkeys perform object-based saccades, the movement vector can be distinguished from the activity related to the object, even when the object is flashed on just prior to the eye movement. In antisaccade trials it has been claimed that there is activity related to the visual target and activity related to saccades, and thus they cannot be separated (Gottlieb and Goldberg, 1999). However, subsequent studies showed that the visual and movement activities exist in different populations of LIP cells and can in fact be easily distinguished (Zhang and Barash, 2000).

Although action-related activity is well established in PPC, a legitimate question is whether this activity is related to plans to make movements or instead reflects predicted changes in sensory input arising from the integration of efference copy. Probably both are in operation. The persistent activity in LIP and PRR on delay tasks has been shown not to reflect the sensory memory of targets or attention (Gnadt and Andersen, 1988; Mazzoni et al., 1996; Snyder et al., 1997, 1998; Batista and Andersen, 2001). Since it can precede the actual eye or arm movement by many seconds, it would appear to reflect the plan to move. However, there are additional changes in activity, both in the spiking and local field potentials that occur around the time of the movement, that likely reflect, among other possibilities, a prediction of the sensory consequences of movements (Andersen et al., 1987; Barash et al., 1991; Pesaran et al., 2002).

Reading out intended reaches

An interesting test of the idea that movement plans are conveyed in the activity of PPC neurons is to determine whether animals can use these plan-related signals to control external devices (Wessberg et al., 2000; Serruya et al., 2002;

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Taylor, Tillery, and Schwartz, 2002; Shenoy et al., 2003; Musallam et al., 2004). This research, while important from a purely scientific viewpoint, also serves the therapeutic application of developing a neural prosthetic that can be used for paralyzed patients.

PRR SIGNALS The PRR defined in early studies included the medial intraparietal area (MIP) and the dorsal aspect of the parietal occipital area (PO) (Snyder et al., 1997). It is similar to LIP in many aspects, the major difference being that it is active when monkeys plan arm movements, whereas LIP is most active when they plan eye movements. One of the most interesting similarities between these areas is that both code very different movement plans (reaches vs. saccades) in retinal coordinates (Stricanne et al., 1996; Batista et al., 1999; Cohen and Andersen, 2000a, b). Other similarities include shifts of activity within the retinotopic map to compensate for eye movements (Gnadt and Andersen, 1988; Duhamel et al., 1992; Batista et al., 1999), persistent activity for delayed movements (Gnadt and Andersen, 1988; Snyder et al., 1997), and activity for only the next movement in a sequence (Mazzoni et al., 1996; Batista and Andersen, 2001).

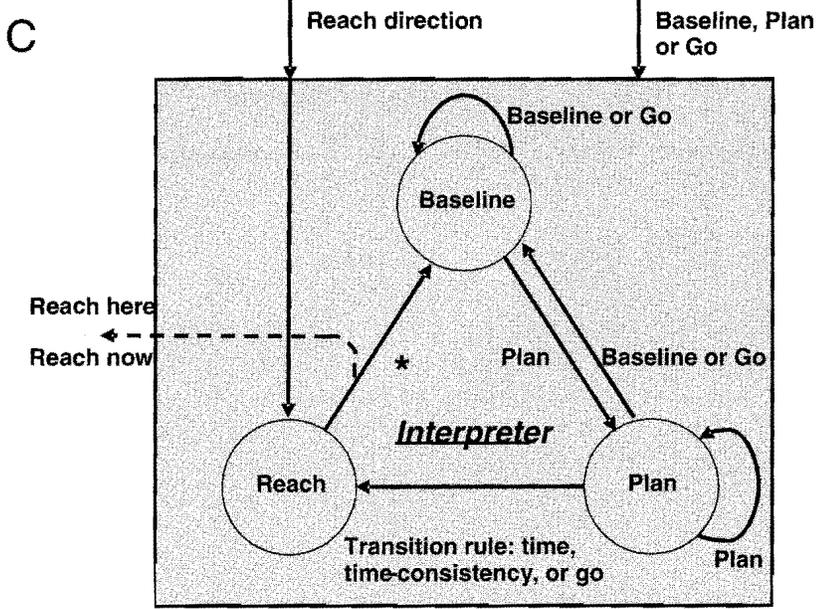
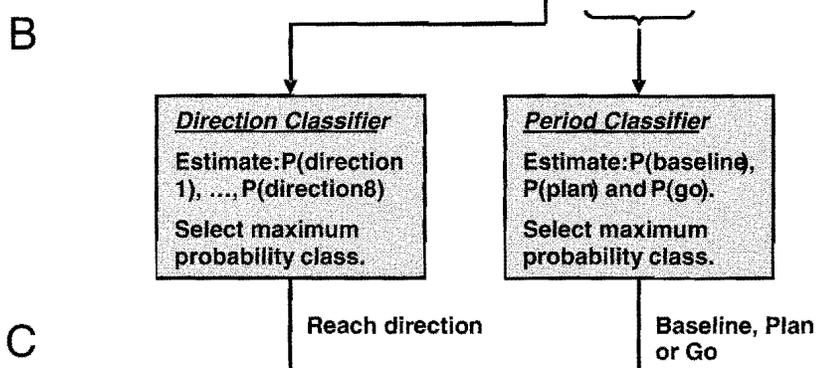
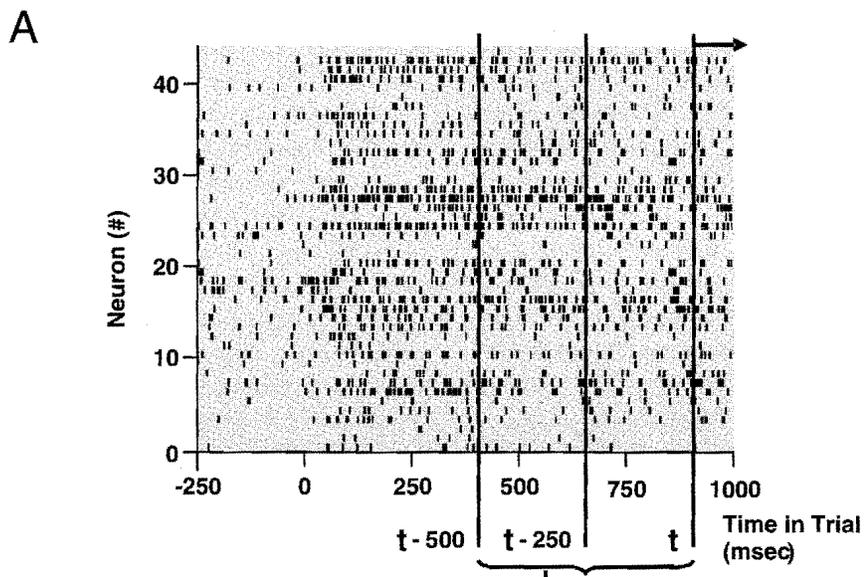
We reasoned that if PRR has activity related to the intention to make limb movements, then monkeys could use this plan signal to move a cursor on a computer screen by thinking about the movement but not executing it. In a recent study we examined whether we could decode where and when monkeys planned to make arm movements (Shenoy et al., 2003). We analyzed the activity of cells that had been recorded, one at a time, from PRR. In this task, the monkeys plan arm movements in different directions, but withhold their response until a go signal. If the target is within the response field of the cell being recorded, there is typically a visual response to the target, persistent “hold” activity related to the plan to move, and an additional increment above the hold activity just prior to and during the movement.

Figure 34.1 shows the computational architecture of a state machine that was designed to predict when an animal is planning a reach, where it intends to reach, and when it intends to execute the planned reach. Figure 34.1A shows the activity of one trial from each of 41 cells recorded from PRR of one monkey for a reach in a single direction. Two sliding window classifiers estimate the *direction* and *period* using maximum likelihood decoders (figure 34.1B). The classifier signals are fed to an *interpreter* (figure 34.1C) that determines when and where a reach should be generated. The interpreter transitions through different states and uses transition rules to improve performance. Using this decoder, performance for predicting reaches in any of eight directions exceeds 90% with as few as 40 neurons.

In the above experiments the analysis was performed off-line. In a recent study we have performed “closed-loop” experiments in real time (Meeker et al., 2002). In these studies single cells are recorded from PRR and their directional tuning is determined using the delayed-reach task. The two directions that give the statistically most distinguishable responses are chosen, and the experiments are performed again in those two directions. However, on this second set of trials the memory activity is used to predict the direction in which the monkey is planning to reach, even though no reach is actually performed. This prediction is based on the response of the cell, as well as on the data recorded during the previous set of trials using real reaches. In a subset of the trials, at the end of the delay period a cursor is placed in one of the two possible locations as predicted by the neural activity during that period. Overall, the animals were able to correctly position a cursor on about 70% of the trials, but for many cells they operated nearly perfectly. However, the most interesting finding was that during the cursor-control period of the task, when the monkey was not making reaches, about one third of the cells improved their direction tuning. This effect was fast, taking only tens of trials.

FIGURE 34.1 Computational architecture for generating high-level cognitive control signals from PRR premovement, plan activity. (A) Spike raster for each PRR neuron contributing to the control of the prosthetic device as a function of time in the delayed, center-out reach task. A single trial is illustrated. The visual target, specifying the eventual reach goal, occurs at 0 ms. The onset of arm movement occurs after 1100 ms (not shown). (B) Classifiers use neural activity from finite-duration sliding analysis windows to estimate the direction of arm movement (*direction classifier*) and the current neural/behavioral period (*period classifier*). Both classifiers first calculate the probability of each class, and then select the most probable class for subsequent use. (C) The *interpreter* receives the stream of period classifications (i.e., baseline, plan, or go) from the period classifier and the stream of real direction classifications (e.g., downward reach) from the direction classifier. The interpreter con-

sists of a finite-state machine that transitions among three states (baseline, plan, and reach) according to the period classification at each time step. Three different rules for transitioning from the plan state to the reach state (time, time consistency, and go) are considered. Once in the reach state, the interpreter always transitions back to the baseline state at the next time step in order to prepare for the next reach. During this transition, a high-level, cognitive control signal is issued stating that a reach should occur immediately to the location specified by the direction classifier's current estimate. More sophisticated interpreters may include additional states and may use additional signals (e.g., band-limited LFP power) to govern transitions. (Reprinted with permission from K. V. Shenoy et al., Neural prosthetic control signals from plan activity. *Neuroreport* 14:591–596. © 2003 by Lippincott Williams & Wilkins.)



* This transition causes a high-level, cognitive control signal to be issued stating: reach here (from direction classifier), reach now.

Since paralyzed patients cannot reach to calibrate a prosthetic system, the rapid plasticity seen in PRR is very promising and suggests that patients may be able to rapidly learn to control the prosthetic. This rapid plasticity may reflect the fact that PRR is at the interface between sensory and motor representations, and this adaptability may help to keep these representations in proper spatial register. Studies using prismatic adaptation paradigms suggest that PPC, along with the cerebellum, plays a major role in this calibration process. Recently, we have expanded this study to the examination of activity from many simultaneously recorded cells, with the animals positioning the cursor in more than two locations (Cornell, Mussallam, and Andersen, 2003; Musallam et al., 2003, 2004).

LOCAL FIELD POTENTIALS Figure 34.2 shows activity recorded from a neuron in area LIP, the eye movement area adjacent to PRR (Pesaran et al., 2002). The animal was performing a memory saccade task, the timing of events shown

in figure 34.2A. During the memory period the cell is very active when the monkey is planning to saccade into the response field of the neuron (upper panel of figure 34.2B). The lower panel shows part of the memory period expanded in time. Not only are spikes present during the delay, but there is also an oscillation in the local field potential (LFP). The spikes ride on top of the peaks in the LFP oscillations. The oscillation is generally in the range of 25–90 Hz, that is, in the so-called gamma band. It is produced by groups of cells around the electrode tip contributing to an averaged field potential. These oscillations are believed to be due primarily to excitatory postsynaptic potentials, which are synchronized in the local population of cells. The coherence of the spiking with the LFP is likely a result of this oscillating excitatory drive. Figure 34.2C shows traces for the same cell, but for saccades planned outside of the cell's response field. Of note, there are many fewer spikes during the delay period (upper panel), and the oscillatory LFP is also much reduced. The directional tuning of the LFPs is likely due to the colum-

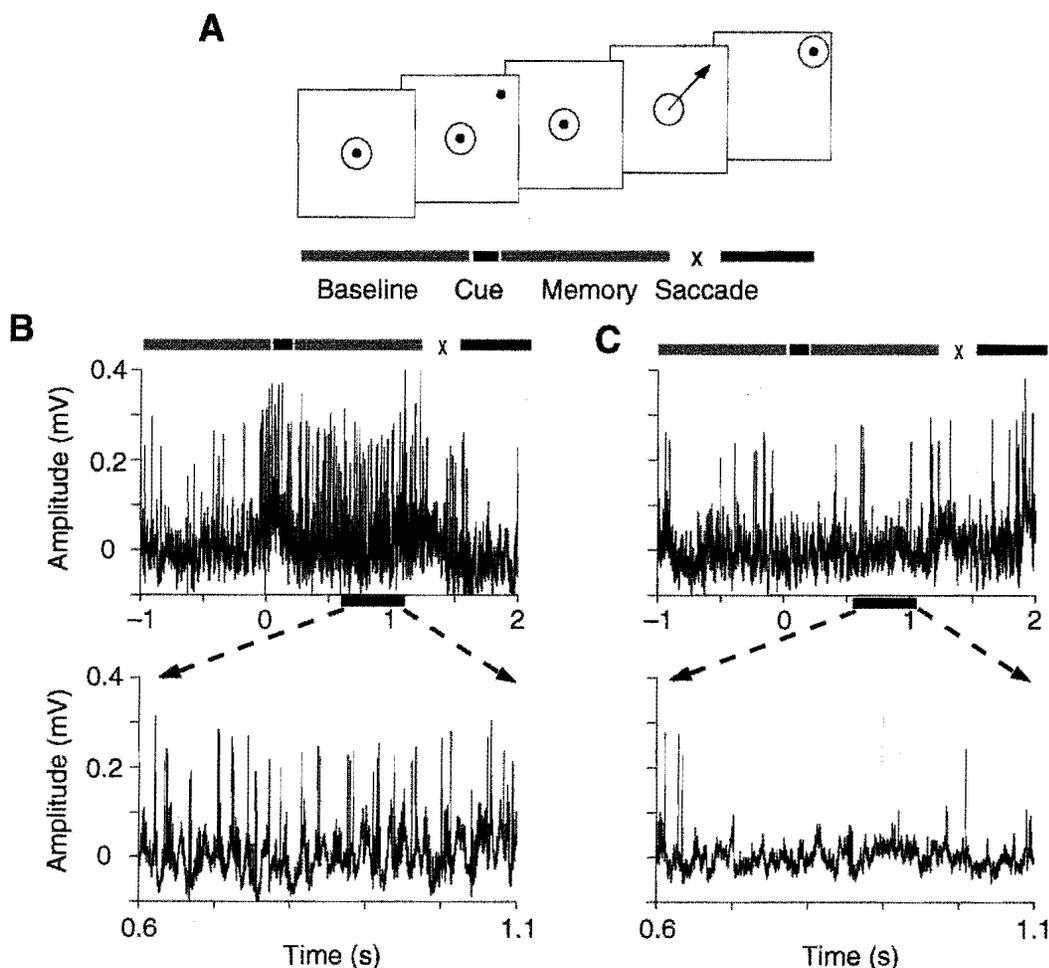


FIGURE 34.2 The memory saccade task. (A) The monkey performs a memory saccade in one of eight saccade directions. (B) Sample trace of extracellular potential for a trial during a saccade in the preferred direction. The polarity of the potential is reversed.

The data are viewed on an expanded time base during the memory period from 0.6 to 1.1 s—below. (C) Sample trace for a saccade in the antipreferred direction. (From Pesaran et al., 2002.)

nar organization for saccade direction that is known to exist in LIP (Pezaris et al., 1998).

The gamma band oscillation in LIP was found to be a good predictor of the direction in which monkeys planned to make saccades. Interestingly, another oscillation was also present in the beta band, centered at around 20 Hz. This oscillation was not direction tuned but rather indicated the behavioral state of the animal. When the animal was planning a saccade it slowly increased, while at the time of the eye movement it dramatically dropped to low amplitude (Pesaran et al., 2002).

From a neural coding point of view, these oscillations are of great interest. Their presence indicates that cells code the direction and state of the animals not only in the rate of action potentials, but also in the power of the local field oscillations. A similar temporal structure was also found in the spectrum of the spike trains. Thus, there are dynamic, temporal response fields that potentially could be “read out” by downstream structures, much like the rate. However, the functional role of these oscillations is not yet known.

From a practical point of view, these oscillations are extremely useful for neural prosthetics applications. A major challenge for cortical prosthetics is to acquire meaningful data from a large number of channels over a long period of time. This is particularly challenging if single spikes are used, since typically only a fraction of probes in an implant array will show the presence of spikes. Moreover, these spikes are difficult to hold over very long periods of time. However,

since local fields come from a less spatially restricted listening sphere, they should be easier to record and hold. In fact, it has been our experience that they can be recorded from most probes, and the recordings can last for at least as long as 2 years. Thus, it would be of great advantage to be able to use the LFPs for decoding when and where monkeys intend to make movements.

In recent experiments we directly compared decodes using spikes and LFPs obtained from LIP (Pesaran et al., 2002). A linear discriminant analysis was used to predict, from single trials, the direction of a planned movement (preferred vs. antipreferred direction, figure 34.3A). The performance for predicting direction was similar for spikes and LFPs. The correct prediction rate for the preferred direction was 87% for spikes and 87% for LFPs, and for the antipreferred direction 78% for spikes and 87% for LFPs. We also examined decoding the state (plan vs. execution state, figure 34.3B). The LFPs were better for this decode. The plan state was correctly identified 56% of the time for spikes and 71% for LFPs, and the execution state was correctly identified 57% of the time for spikes and 71% for LFPs. The better performance of the LFP state decodes may reflect the activity due to circuits within LIP or inputs to LIP from external sources. Further work will be required to distinguish between the two.

We have recently begun to characterize gamma band temporal structure in PRR as well (Scherberger et al., 2003). The gamma band temporal structure in PRR is also

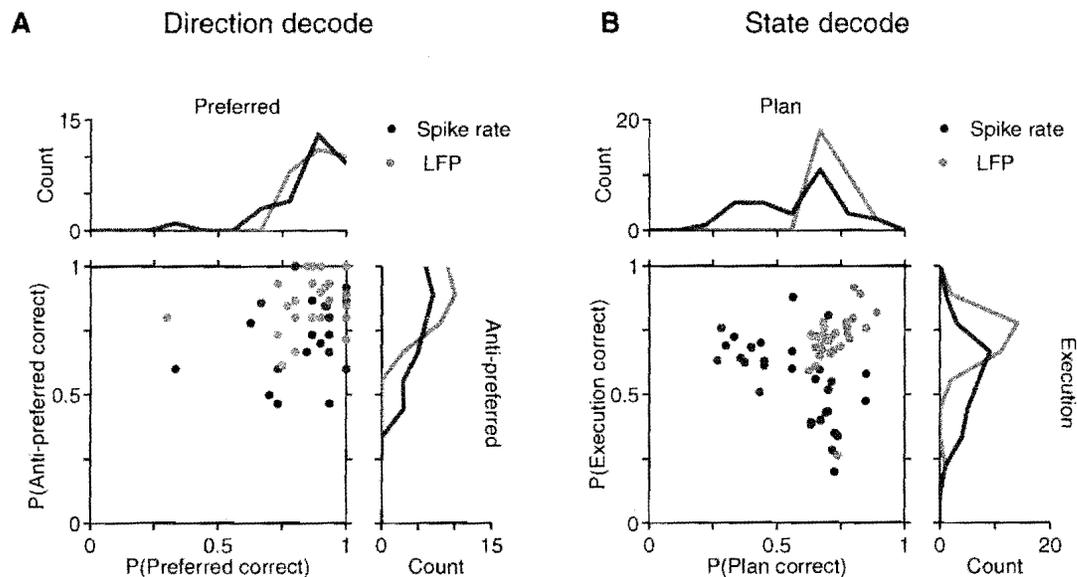


FIGURE 34.3 Single trial decode of a movement plan. (A) Direction decode using spike rate (dark gray) and the LFP spectrum (light gray). Each dot represents a single cell or site. Horizontal axis is the probability that a saccade in the preferred direction is decoded correctly. Vertical axis is the probability that a saccade in the anti-preferred direction is decoded correctly. Line plots show the

histograms for cell/site counts for each direction. (B) State decode. Horizontal axis is the probability that the activity from the plan state is decoded correctly. Vertical axis is the probability that the activity from the execution state is decoded correctly. Line plots show the histograms for cell/site counts for each state. (From Pesaran et al., 2002.)

direction tuned for the spikes and LFPs, but the peak power in the spatially tuned frequency band is 10–20 Hz lower in PRR than in LIP.

From both scientific and practical points of view, an important recent development was the identification of a homologue of PRR in the human (Connolly, Andersen, and Goodale, 2003; figure 34.4). In these experiments human subjects performed delayed saccades and delayed pointing, similar to delayed saccade and reach experiments that we have performed in monkeys. Using event-related functional magnetic resonance imaging, we were able to localize an area in parietal cortex that responded preferentially during the memory delay trials for planning pointing movements compared to saccades.

The PRR in humans has attributes that are different from motor cortex, which may be useful for deriving control signals for neural prosthetics. The main sensory feedback to motor cortex is from somatosensory inputs, whereas the major sensory feedback for PRR appears to be visual. Often, somatosensory feedback is lost with paralysis, whereas vision is not. Thus, feedback for evaluating terminal movement errors may be more naturally conveyed to PRR. In addition, the remarkable plasticity we have seen in PRR during cursor-control tasks bodes well for this region's ability to learn to control external devices. PRR is also more removed from motor areas, which undergo pathological changes with paralysis. Thus, it is possible that PRR will be more resilient to the changes that result from disuse following direct damage to corticospinal projections (as in spinal cord injury).

Coordinate transformations

Perceptually we have a good sense of where things are in the world, and behaviorally we can effortlessly use sensory

stimuli to guide movements of a variety of body parts. These observations suggest that space is represented in many coordinate frames in the brain for perception and action. Interestingly, though, when neuroscientists have recorded from various sensory and motor representations in the brain, they have found that these representations are not simple maps containing receptive fields in a particular coordinate frame. For instance, areas in the sensorimotor pathway for visually guided movements often contain retinal response fields that are gain modulated by body position signals (Andersen et al., 1985; Salinas and Thier, 2000). Still other areas contain response fields that are partially shifted between retinotopic and other reference frames (Striccanne et al., 1996; Duhamel et al., 1997; Cohen and Andersen, 2000a, b; Buneo et al., 2002). One advantage of the “gain field” representation is that information in multiple reference frames can be represented simultaneously. Another is that information is not lost; for instance, cells that code head-centered locations using gain modulation still contain information about the retinal location of the target. Neural network models have demonstrated that this gain field mechanism can be used for coordinate transformations (Zipser and Andersen, 1988; Pouget and Sejnowski, 1995; Pouget and Snyder, 2000; Xing and Andersen, 2000a, b).

The fact that gain modulation is found in a variety of brain areas and seems to operate in a number of functional contexts suggests that its computational function may extend well beyond sensorimotor transformations and may be a general method for neural computation when transformations between brain representations are required (Salinas and Thier, 2000). Recently, we have examined whether gain modulation is reflected in human visual perception, and if it is psychophysically detectable (Nishida et al., 2003). In particular, we wished to determine the coordinate frames in

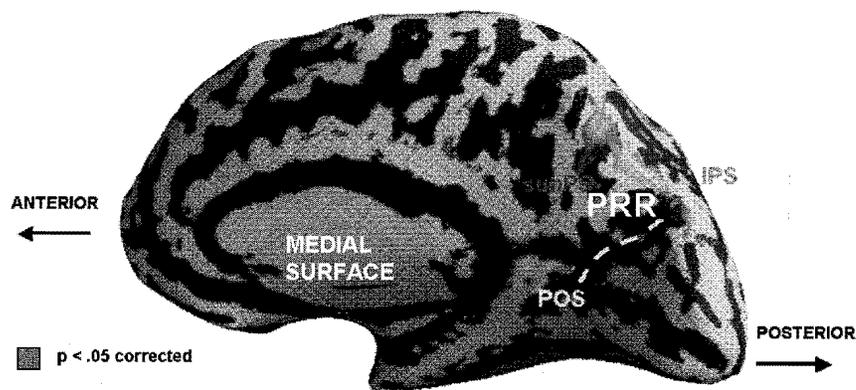


FIGURE 34.4 Medial view of an inflated cerebral cortex, showing unfolded sulci and gyri and the location of the fMRI delay interval activation, as determined using multiple regression analysis (ten subjects, $P < 0.05$). GLM signal timecourses that were subjected to further ANOVA analysis were situated anterior to the parieto-

occipital sulcus, posterior to the subparietal sulcus, medial to the intraparietal sulcus. (Reprinted with permission from J. D. Connolly et al., fMRI evidence for a “parietal reach region” in the human brain. *Exp. Brain Res.* 153:140–145. © 2003 by Springer-Verlag.) (See color plate 16.)

which various perceptual phenomena may be represented in cortex.

To assess the effect of gaze on human visual perception, we examined gaze-dependent visual aftereffects. In these experiments subjects were adapted in one gaze direction and then tested in the same or a different gaze direction. In both same and different (opposite) gaze directions, the images of the test stimuli on the retinas were identical.

Figure 34.5a shows that small but significant differences were found for a wide variety of aftereffects, including the motion aftereffect (MAE), tilt aftereffect (TAE), and the size aftereffect (SAE). In all cases the aftereffect was greater for the same gaze direction compared to the opposite gaze direction by about 15% (figure 34.5b). The detection threshold elevation showed the same trend (see figure 34.5b) but did not reach statistical significance (see figure 34.5a), largely owing to greater variability of the effect.

These experiments suggest that gaze modulates visual activity in areas of striate and extrastriate cortex that are known to play a role in the percepts of motion, orientation, and size. In other experiments the aftereffects were tested for world- and object-centered effects. In the world-centered coordinate test, TAE magnitudes were compared between locations in space that were adapted by the test stimulus prior to testing at a different gaze direction. No aftereffect was found for retinally nonadapted loci that occupied the spatial location of the test stimulus after the gaze shift. Since the subjects did not shift their heads or bodies in this experiment, this study also indicates that head- or body-centered effects were not present. In the object-centered test, the test stimulus reappeared at the same world-centered location as the adaptation and then moved to a new location. No transfer of adaptation was found in this experiment.

The world- and object-centered tests were negative, which suggests that, at least for the TAE, the perception of orientation does not undergo a complete transformation from a retinotopic to a nonretinotopic representation anywhere in

the brain. Of course, there may be higher-level percepts that do undergo these transformations, particularly those more closely linked to motor systems. This question is an interesting topic for future research.

OBJECT-BASED SACCADDES Lesions of the PPC in humans can produce object-fixed neglect, in which patients are unaware of the contralateral side of objects (Driver and Halligan, 1991; Behrmann and Moscovitch, 1994; Driver et al., 1994; Hillis and Caramazza, 1995). This result suggests that cells in PPC might code parts of an object in an object-based reference frame. In many experiments examining saccade-related neural structures, single spots of light are used to examine the response properties of neurons. This approach has been the case for area LIP, and it has been reported that the neurons in this area code visual targets, plans for eye movements, and saccade-related responses all in retinotopic coordinates (Andersen and Buneo, 2002). However, in natural situations, the pattern of eye movements is based on parts of objects and spatial relations between objects. Several studies have examined eye movement areas in the frontal and parietal cortex using tasks in which animals make eye movements to objects with particular features among groups of distracter objects (Bichot et al., 1996; Gottlieb et al., 1998; Bichot and Schall, 1999; Hasegawa, Matsumoto, and Mikami, 2000; Constantinidis and Steinmetz, 2001). In one experiment in the supplementary eye fields (SEF), target selection was studied within objects, and it was reported that the response fields of the neurons were in an object-fixed reference frame (Olson and Gettner, 1995).

Given the prevalence of object-fixed neglect in the PPC, we decided to examine the coordinate frame used to make object-based saccades by LIP (Sabes, Breznen, and Andersen, 2002). In this task, a filled polygon was used as the test object. On each trial, the monkey was presented with this polygon in one of a variety of possible orientations. One

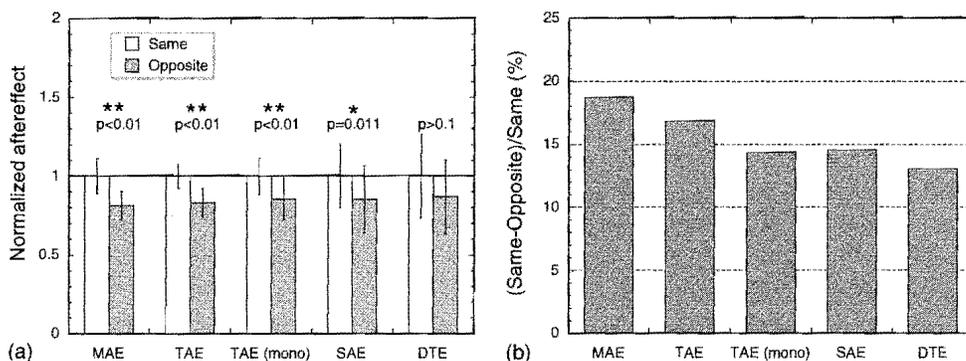


FIGURE 34.5 The graph shows the modulation ratio, defined as the contrast ratio of adaptation between the same and opposite directions of gaze. Gaze angle had a constant effect of around 15%

for all types of adaptation tested. (Reprinted with permission from S. Nishida et al., Gaze modulation of visual aftereffects. *Vision Res.* 43:639–649. © 2003 by Elsevier.)

of four fingers on the object was indicated by a flashed cue, and the monkey memorized the location of the cue. The object then disappeared briefly and reappeared at a new orientation. At this point the animal was required to saccade to the end of the previously cued finger in order to receive a drop of juice reward.

We found that LIP neurons code the retinotopic location of the target and the retinotopic orientation of the object. No cells were specific for a finger, that is, for coded locations on the object in object-based coordinates. Individual cells were sensitive to target location, others to orientation, and some cells to both. Moreover, there was a dynamic evolution for tuning in the population, with about equal numbers of cells coding orientation and target location at the beginning of the task and many more cells coding the retinotopic location of the target later in the task, near the time of the saccade.

One possible explanation of the object-based neglect after parietal lesions is that it results from damage to a population of neurons, none of which carry explicit information about location in object coordinates but do so as an ensemble. Computational models have made exactly this point. Alternatively, it may be that the projection of PPC onto SEF and other frontal lobe structures results in the explicit representation of targets in object-fixed coordinates. We have begun examining this possibility by performing a variant of the object-based saccade task and recording from SEF neurons.

Cells with both orientation and target tuning could be separated using a general linear model (Sabes, Breznen, and Andersen, 2002). This was accomplished by probing cell activity using only an object, or only a target for a saccade. When animals performed the object-based saccade task, it was found that, for cells with object orientation and target location sensitivity, the two components of activity added linearly. Interestingly, the target and orientation components could be easily separated even when the object reappeared at the new orientation. The go signal to make the saccade was given simultaneously with the reappearance of the object. Although the object's reappearance invoked a large visual response that indicated the orientation of the object, the direction of the planned movement could still be read out at all times. This readout of the two variables was demonstrated by computing population vectors for both variables (Breznen and Andersen, 2000). Thus, recent claims that movement plans cannot be distinguished from visual responses in LIP are incorrect (Powell and Goldberg, 2000; Goldberg et al., 2002; Bisley and Goldberg, 2003).

DIRECT COORDINATE TRANSFORMATIONS USING GAIN FIELDS

The coordinate transformation for visually guided reach movements requires that the eye-centered visual inputs be transformed to a limb-centered goal of the intended direc-

tion and amplitude of the movement. There are at least three ways in which this computation can be performed, as illustrated in figure 34.6. One is a sequential model (figure 34.6*a*), in which the transformation occurs in stages (Flanders et al., 1992; Henriques et al., 1998; McIntyre et al., 1998). The eye-centered location of the visual target is first combined with an eye position signal to form a representation of the target in head coordinates. Then head position information is added to form a representation in body-centered coordinates. Finally, the body-centered position of the hand is subtracted from the body position location of the target to generate a hand-centered representation of the target, indicating the motor error for acquiring the target. Psychophysical results suggest that such a sequential representation may be used for certain reach tasks (Flanders et al., 1992; McIntyre et al., 1998). However, this model requires a good deal of neural real estate, including intermediate representations of the reach targets in head- and body-centered coordinates. Recording experiments in the dorsal visual pathway associated with reaching movements have found only small numbers of cells in the ventral intraparietal area (VIP) and PO that use intervening stages such as head-centered representations (Battaglini et al., 1990; Duhamel et al., 1997).

A second, combinatorial model is shown in figure 34.6*b* (Battaglia-Mayer et al., 2000). In this model, all signals of retinal target location, eye position, head position, and limb position converge onto the same area, and the location of the target with respect to the hand is then read out of this high-dimensional representation. There is evidence for such a high degree of convergence within area PO. However, from a computational perspective this model suffers from the "curse of dimensionality," since at least three spatial dimensions of all the four variables must be encoded in this area. If only ten neurons were required along each dimension, even this sparse tiling would require a trillion neurons, about two orders of magnitude more neurons than are found in the cerebral cortex.

A third, direct model (Buneo et al., 2002) is shown in figure 34.6*c* and *d*. In this model the location of the target and the initial location of the hand are both represented in visual, that is, eye-centered, coordinates. The two are simply subtracted to produce a direct transformation of the target in hand coordinates. Such a method requires many fewer neurons, only 1 million by the above calculation, and thus does not suffer as much from the curse of dimensionality.

Recently, we have found evidence for this direct model in the PPC (Buneo et al., 2002). The PRR neurons code the location of reach targets in eye coordinates (Batista et al., 1999), and the initial position of the hand produces a gain modulation of the response. As indicated in the left part of figure 34.7, this gain modulation is also in eye coordinates. By converging inputs of cells with these gain fields onto cells

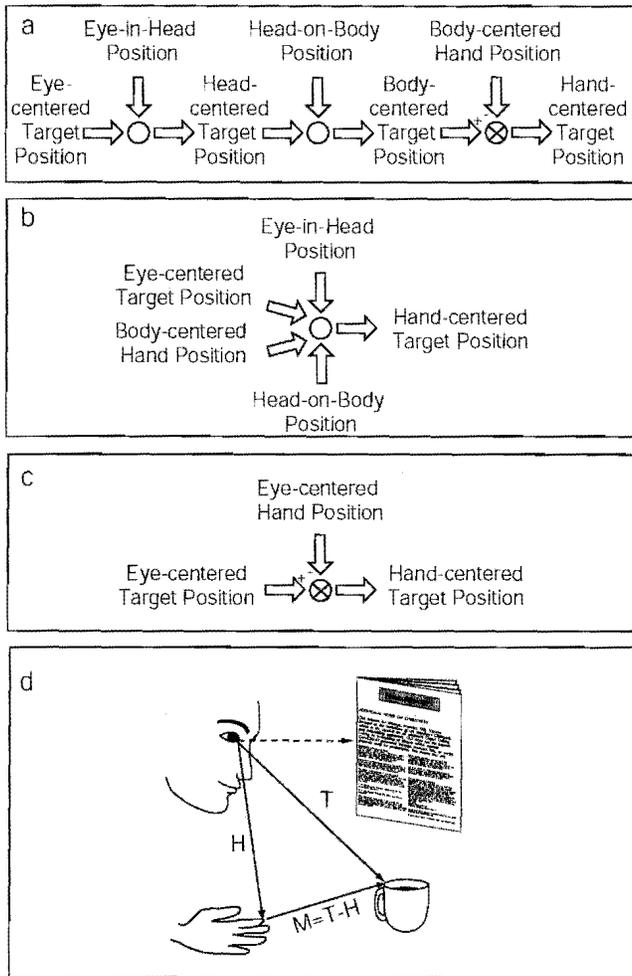


FIGURE 34.6 Schemes for transforming target position from eye-centered to hand-centered coordinates. (a) Sequential method. (b) Combinatorial method. (c) Direct method. (d) Illustration of reaching for a cup while fixating a newspaper, using the direct method. The position of the cup with respect to the hand (M) is obtained by directly subtracting hand position (H) from target position (T), both in eye coordinates. (Reprinted with permission from R. A. Andersen and C. A. Buneo, Sensorimotor integration in posterior cortex. In *The Parietal Lobes*, A. M. Siegel, R. A. Andersen, H.-J. Freund, and D. D. Spencer, eds. Baltimore: Lippincott Williams & Wilkins, pp. 159–177. © 2003 by Lippincott Williams & Wilkins.)

in other cortical areas, the subtraction of target- and hand-related signals can be accomplished (right part of figure 34.7). Thus, the convergence of inputs from PRR neurons onto premotor cortex could conceivably produce this transformation in one step. In area 5 we have found that cell response fields are partially shifted between eye and limb coordinates (Buneo et al., 1998). Again, this representation can be produced by a one-step convergence from PRR neurons. The reason for the partially shifted profile of area 5 cells may reflect the coordinate representation that is necessary for the computations performed by this area. Consis-

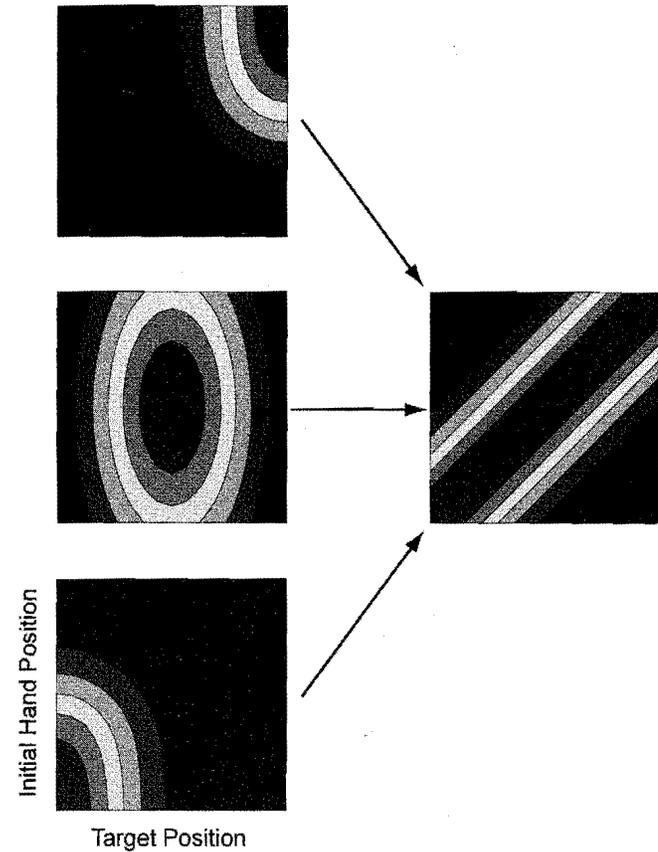


FIGURE 34.7 Schematic of how three PRR neurons, coding reach targets in eye coordinates and gain modulated by the initial hand position in eye coordinates, could converge onto another neuron to produce a receptive field in limb coordinates.

tent with this idea is the fact that area 5 receives visual signals, represented in eye coordinates, and efference copy signals and proprioceptive signals, represented in limb coordinates. Thus, the representation in area 5 may be optimal for making computations that use these different signals.

The use of coordinate transformation schemes may be context dependent. For instance, in the experiments of Buneo and colleagues, the initial position of the hand was visible to the animal, and thus a direct retinal subtraction may be the most parsimonious solution (Buneo et al., 1998). In other conditions where the hand is not visible a sequential model may be used (Flanders et al., 1992; McIntyre et al., 1998). We are currently performing experiments to distinguish between these possibilities.

SHARED BEHAVIORAL REFERENCE FRAME FOR TARGET SELECTION FOR REACHES AND SACCADDES It would be parsimonious to represent arm and eye movements in the same coordinate frames, given the close coupling of these two types of action. The mere fact that so many eye movements are made compared with number of limb movements would

suggest that an eye-centered reference frame be used. In fact, as reviewed above, PRR codes the locations of reach targets in eye coordinates (Batista et al., 1999). Also, the initial location of the hand is coded in eye coordinates in PRR and exerts its influence as a gain modulation of the target-related activity (Buneo et al., 2002).

Inspired by the above findings, we have recently examined the behavioral reference frame used by monkeys performing a hand/eye coordination task (Scherberger, Goodale, and Andersen, 2003). The influence of eye, head, and body position on target selection was examined for both eye and hand movements. We found that the initial position of the eyes in the orbits biased the monkey's choice. This finding was not surprising, insofar as the preferred direction was one that always tended to center the eyes in the orbits. This preference reduces the effort of maintaining the eyes at peripheral fixation angles, and also provides a more optimal operating range for subsequent eye movements. Also not surprising was the finding that the limb used also biased the decision, with rightward movement preferred for the right limb and leftward movement preferred for the left. What was counterintuitive was the finding that the positions of the eyes in the orbits influenced the selection of the reach direction, with the animals choosing to reach to targets that were closer to the fixation position. However, the orientation of the trunk showed much less effect on the selection. While the eye position had considerable effect on selection of reach targets, the arm position did not have an influence on the choice of saccade targets.

These experiments show behavioral evidence for a common reference frame for hand/eye coordination, at least for target selection. The results indicate that the eyes play a more dominant role, consistent with the eye-centered representations for reaches and saccades found in PPC. Technically, the reaches and saccades are chosen on the basis of head-centered coordinates; however, this decision can easily be accomplished by the eye position gain modulation of retinocentric representations that are found in parietofrontal cortical areas. Moreover, these decisions would bring targets more into the operating range of the cortical eye-centered representations. We are currently performing experiments to see where eye position signals exert their effect on the decisions made in this task.

Conclusion

This chapter has focused on two functions of PPC in sensorimotor transformations, the planning of movements and coordinate transformations. We have shown experimentally that parietal activity related to reach planning can be read out and used by monkeys to control a cursor on a monitor without reaching movements. These experiments are real-time and direct demonstrations that signals related to plan-

ning in the PPC can be used by the animals to control external devices. Moreover, the neural activity used for control is highly malleable by the animals, and they can rapidly adjust to increase their performance in closed-loop experiments. We also found that LFP activity can be used to decode the intentions of the monkeys. A practical advantage of using LFPs compared to spikes is the relative ease of recording and considerable stability over time. The demonstration of cursor control, the finding of rapid plasticity, and the ability to decode movement intentions with LFPs all bode well for the use of PPC as a source of control signals to assist paralyzed patients in neural prosthetics applications.

The PPC also plays an important role in coordinate transformations. The gain field mechanism proves to be a computationally efficient method for realizing these transformations. However, the gain field mechanism may also act more broadly in a variety of computations. New evidence for this broader applicability is the finding of eye position gain effects on a variety of visual percepts in humans.

In a new class of experiments, we examined whether object-centered coding is used by area LIP in a saccade task that requires the use of object-based information. We found that the orientation of the object and the target location on the object are both encoded in retinal, and not object-centered, coordinates. However, reminiscent of other gain field results, this information is all that is required to solve the task, and the explicit representation of the target in object-centered coordinates may not be required.

We have also found that the conversion from eye to limb coordinates for visually guided reach movements may occur in a direct fashion, one that can bypass intermediate head- and body-centered representations. Again, this transformation is accomplished with gain fields, but in this case the gain field is the target location, modulated by initial hand position, both represented in retinal coordinates. This type of gain field was found in PRR. We have also found behavioral results consistent with this eye-based coding of early reach plans. The selection of reach and saccade targets was found in monkeys to be highly biased by the position of the eyes, and reach targets were found to be much less affected by trunk position. Moreover, the position of the limb did not affect the choice of saccade targets.

Research in the PPC continues to be a fertile ground for studying how sensorimotor transformations are accomplished. The finding of possible human homologues of PRR, LIP, and AIP with fMRI experiments points to the use of fMRI in monkeys in the future as a powerful method to directly compare monkey and human results. Also, experiments that can read out and read in information to the PPC will be invaluable in providing direct tests of models of parietal lobe function. The future is bright for sensorimotor research.

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