

The posterior parietal cortex: Sensorimotor interface for the planning and online control of visually guided movements

Christopher A. Buneo^{a,*}, Richard A. Andersen^b

^a Harrington Department of Bioengineering, Arizona State University, P.O. Box 879709, Tempe, AZ 85287-9709, USA

^b Division of Biology, California Institute of Technology, Mail Code 216-76, Pasadena, CA 91125, USA

Received 14 June 2005; received in revised form 15 September 2005; accepted 11 October 2005

Available online 21 November 2005

Abstract

We present a view of the posterior parietal cortex (PPC) as a sensorimotor interface for visually guided movements. Special attention is given to the role of the PPC in arm movement planning, where representations of target position and current hand position in an eye-centered frame of reference appear to be mapped directly to a representation of motor error in a hand-centered frame of reference. This mapping is *direct* in the sense that it does not require target position to be transformed into intermediate reference frames in order to derive a motor error signal in hand-centered coordinates. Despite being direct, this transformation appears to manifest in the PPC as a gradual change in the functional properties of cells along the ventro–dorsal axis of the superior parietal lobule (SPL), i.e. from deep in the sulcus to the cortical surface. Possible roles for the PPC in context dependent coordinate transformations, formation of intrinsic movement representations, and in online control of visually guided arm movements are also discussed. Overall these studies point to the emerging view that, for arm movements, the PPC plays a role not only in the inverse transformations required to convert sensory information into motor commands but also in ‘forward’ transformations as well, i.e. in integrating sensory input with previous and ongoing motor commands to maintain a continuous estimate of arm state that can be used to update present and future movement plans. Critically, this state estimate appears to be encoded in an eye-centered frame of reference.

© 2005 Elsevier Ltd. All rights reserved.

Keywords: Eye movements; Arm movements; Spatial representation; Coordinate transformations; Motor control

1. Introduction

What role does the posterior parietal cortex (PPC) play in visually guided behavior? This question has been the subject of much research since Vernon Mountcastle and colleagues described in elegant detail neural activity in the PPC related to movements of the eyes and limbs (Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975). Although Mountcastle and colleagues interpreted this activity as serving largely movement functions, others interpreted similar activity as reflecting higher order sensory or attentional processes (Robinson, Goldberg, & Stanton, 1978). Using experiments designed to control for sensory and movement related activity, Andersen and colleagues showed that the PPC has both sensory and motor properties (Andersen, Essick, & Siegel, 1987). They proposed

that the PPC was neither strictly sensory nor motor, but rather was involved in sensory-motor transformations. Findings since this time are consistent with this view, although not always interpreted as such (Bisley & Goldberg, 2003; Bracewell, Mazzoni, Barash, & Andersen, 1996; Calton, Dickinson, & Snyder, 2002; Colby & Goldberg, 1999; Gottlieb & Goldberg, 1999; Mazzoni, Bracewell, Barash, & Andersen, 1996; Powell & Goldberg, 2000; Snyder, Batista, & Andersen, 1997, 1998, 2000; Zhang & Barash, 2000).

A good deal of research in recent years has focused on the lateral intraparietal area (LIP), which serves a sensory-motor function for saccadic eye movements. As with other areas of the brain, sensory attention and eye movement activation appears to overlap extensively in LIP (Corbetta et al., 1998; Kustov & Robinson, 1996). However, when sensory and motor vectors are dissociated explicitly, both sensory and motor related activity are found in LIP (Andersen et al., 1987; Gnadt & Andersen, 1988; Zhang & Barash, 2000), though other tasks have shown that the prevalence of the latter increases as movement onset approaches

* Corresponding author. Tel.: +1 480 727 0841.

E-mail address: cbuneo@asu.edu (C.A. Buneo).

(Sabes, Breznen, & Andersen, 2002). This suggests that LIP might best be thought of as a sensorimotor ‘interface’ for the production of saccades. By interface we mean a shared boundary between the sensory and motor systems where the ‘meanings’ of sensory and motor-related signals are exchanged. In this context, attention could play an important role in limiting activation to that portion of the sensorimotor map that corresponds to the most salient or behaviorally relevant object (Gottlieb, Kusunoki, & Goldberg, 1998).

It is currently unclear whether the PPC plays precisely the same role in the planning and control of arm movements as it does in eye movements. Although similarities in these two behaviors do exist, differences in the biomechanical properties of the eye and arm suggest that the planning and control of these behaviors are quite distinct (Soechting, Buneo, Herrmann, & Flanders, 1995), a fact that may be reflected even in the earliest stages of movement planning. Moreover, considerable differences exist in the neural circuitry subserving these two behaviors, even within the PPC. Strong eye movement related activation is typically restricted to regions of the inferior parietal lobule (IPL), i.e. 7a and LIP, while strong arm movement related activity can be found in both the IPL (7a) and the various subdivisions of the superior parietal lobule (SPL) (Battaglia-Mayer et al., 1998; Caminiti, Ferraina, & Johnson, 1996; Marconi et al., 2001), which include dorsal area 5 (PE), PEc, PEa, and the parietal reach region (PRR), which comprises the medial intraparietal area (MIP) and V6a (Fig. 1). In the remainder of this review, we will focus on the role of the SPL, specifically area 5 and PRR, in the planning and control of reaching. It will be argued that, despite strong differences in the biomechanics underlying eye and arm movements, area 5 and PRR serve an analogous function in reaching as LIP serves in saccades, i.e. that of an interface for sensory-motor transformations. This interface appears to be highly plastic, being modifiable by learning, expected value, and other cognitive factors (Clower et al., 1996; Musallam, Corneil, Greger, Scherberger, & Andersen, 2004).

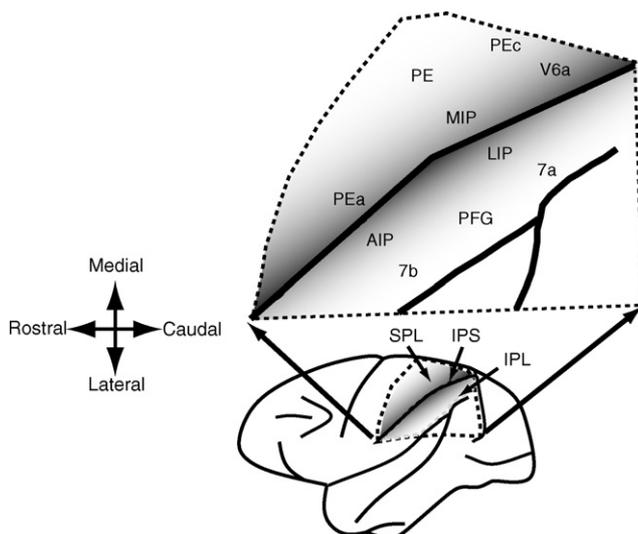


Fig. 1. Lateral view of the macaque monkey brain with the PPC highlighted and expanded. Shaded regions indicate the banks of the intraparietal sulcus (IPS). See text for definitions of abbreviations.

Moreover, we will present evidence that area 5 and PRR, and perhaps other parts of the SPL as well, play a role not only in the inverse transformations required to convert sensory information into motor commands but also in the reverse (‘forward’) process as well, i.e. in integrating sensory input with previous and ongoing motor commands to maintain a continuous estimate of arm state. This state estimate is represented in an eye-centered frame of reference and can be used to update present and future movement plans.

1.1. Definitions

It is useful at this point to explicitly define terms that will be used in the remainder of this review. In order to plan a reaching movement the brain must compute the difference between the position of the hand and the position of the target, i.e. ‘motor error’. Motor error can and may be defined in the motor system in at least two different ways: in terms of a difference in extrinsic or endpoint space, as depicted in Fig. 2, or in terms of a difference in intrinsic space, i.e. as a difference in joint angles or muscle activation levels. In the following section, we start with the assumption that motor error is defined in the PPC in extrinsic space, but we will return to the issue of intrinsic coordinates later in this review.

Hand and target position can each be defined with respect to a number of frames of reference; however, it is currently thought that in order to simplify the computation of motor error, both quantities are encoded at some point in the visuomotor pathway in the same frame of reference. Two possible schemes have been suggested (Fig. 2). In one scheme, target and hand position are coded with respect to the current point of visual fixation—we will refer to this coding scheme as an eye-centered representation, though others have used the terms ‘viewer-centered’,

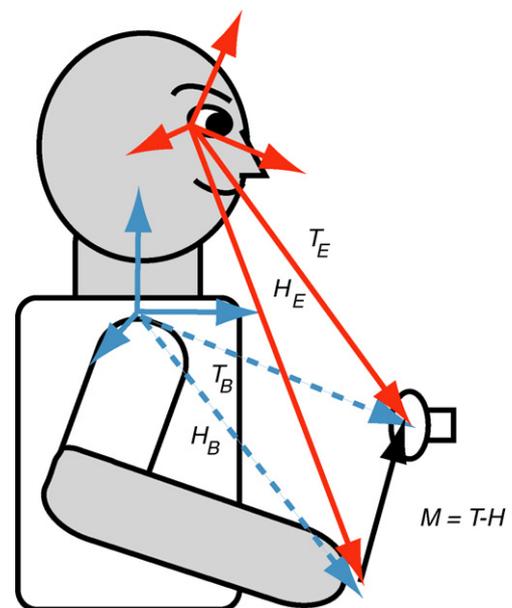


Fig. 2. Schematic showing the reach-related variables described in the text. T , target position; H , hand position; M , motor error; B , body-centered coordinates; E , eye-centered coordinates.

‘gaze-centered’, or ‘fixation-centered’ to describe similar representations (Crawford, Medendorp, & Marotta, 2004; McIntyre, Stratta, & Lacquaniti, 1997; Shadmehr & Wise, 2005). In a second scheme, target and hand position are coded with respect to a fixed point on the trunk; in Fig. 2 this fixed point is at the right shoulder. We will refer to this representation as ‘body-centered’. As illustrated in Fig. 2, both schemes will arrive at the same motor error (M). However, with either scheme a difficulty arises in assigning a reference frame to M . Consider the case where target and hand position are encoded in eye-centered coordinates. Using conventions from mechanics, one could interpret M , the difference between the target and hand, as a ‘displacement vector’ in eye-centered coordinates. Alternatively, this same vector could be interpreted as a ‘position vector’ for the target in hand-centered coordinates. From a purely descriptive point of view, the distinction is arbitrary. However, from the point of view of the neural representation of sensory-motor transformations, this distinction is important and non-arbitrary. In the following sections we will show that some PPC neurons, i.e. those in PRR, appear to encode both target position and current hand position in eye-centered coordinates. As a result, activity in this area could be interpreted as encoding a ‘displacement vector in eye coordinates’. Other PPC neurons appear to encode reach-related variables without reference to the eye; for these neurons the term ‘target position vector in hand coordinates’ or for brevity, ‘target in hand coordinates (Buneo, Jarvis, Batista, & Andersen, 2002)’ appears to be most appropriate. We will also show that some neurons in the PPC do not appear to represent spatial information in a single reference frame but instead are consistent with an encoding of reach-related variables in both eye and hand coordinates, suggesting they play a crucial role in transforming spatial information between these two reference frames.

It is also important to reiterate at this point what is meant by ‘explicit’ and ‘distributed’ representations. As mentioned above, in order to plan a reaching movement both the position of the hand (H) and target (T) must be known. These two signals can be encoded by neurons in the brain in at least two different ways: separably and inseparably. In separable encodings the two variables H and T are ‘independent’ and can be recovered even after being integrated at the single cell level; in other words, target and hand position can be decoded separately from such a representation. With inseparable encodings, the two variables are encoded in a combined form, and are thus ‘dependent’ and cannot be separated. In the current context, separable would mean a representation in which the response of a cell is a function of both target position and current hand position in the same reference frame, but is not a function of the difference between target and hand position. Stated mathematically:

$$fr = f(T) \times g(H) \quad (1)$$

where T is target position and H is current hand position.¹ For brevity, we will refer to neurons that encode reaches in this manner as ‘separable’ neurons and those that encode T and

H inseparably (Eq. (2)) as ‘inseparable’ neurons. To illustrate what the responses of separable (and inseparable) neurons would look like, Fig. 3A depicts a hypothetical experiment in which a fixating monkey makes reaching movements from each of five horizontally arranged starting positions to each of five horizontally arranged targets located in the row directly above the row of starting positions. Movements made directly ‘up’ from each starting position are labeled in this figure with black vectors. Since the vertical component of the targets and starting positions do not vary in this experiment, activity can be analyzed in terms of horizontal components only. The colormaps in Fig. 3B show the responses of several idealized neurons in this experiment, for all combinations of horizontal target and hand position. Activity corresponding to the purely vertical movements shown in Fig. 3A is labeled with white vectors on the colormaps. The leftmost column shows 3 neurons that encode target and hand position separably, in eye coordinates. Each cell is tuned for a target location in the upper visual field but one responds to rightward position (the top cell), another center, and the third leftward (bottom cell). These cells are also tuned for hand locations to the right, center, and left, respectively. In the PPC these responses are often described as a ‘gain field’, in the sense that variations in hand position do not change the tuning for target position but only the overall magnitude or ‘gain’ of the response, and vice versa. Although these neurons respond maximally for a given combination of hand and target position in eye coordinates, they do not in general provide information about motor error in extrinsic space. This information can be obtained however from a suitably large population of such neurons. We will touch on this point again later but suffice to say that a population-based representation of this type would be considered an implicit or ‘distributed’ representation of motor error in extrinsic space, in that the information can only be gleaned from a ‘read-out’ of the population.

Neurons can also encode target and hand position *inseparably*. An example of inseparable coding would be a representation in which the response of a cell is a function of the difference between target and hand position.² Stated mathematically:

$$fr = f(T - H) \quad (2)$$

The rightmost column of Fig. 3 shows the responses of three idealized neurons that encode target and hand position inseparably. These cells respond maximally for a planned movement straight up, but for all positions of the hand in the visual field. In contrast to the separable, eye-centered cells described earlier, these ‘hand-centered’ cells do provide *explicit* information about motor error in extrinsic space. Single neurons that code sensory or motor variables in this way can provide coarse estimates of a percept or a planned action, though populations of such neurons are required to refine these estimates in the face of neural noise (Pouget, Dayan, & Zemel, 2003). Moreover, although such

² Of course, a cell’s response could also be a function of the sum of T and H and still be considered inseparable. However, it is not clear what purpose this representation would serve in reaching and in fact few PPC cells seem to fit such a profile.

¹ In Eq. (1) these signals interact multiplicatively, but they could interact additively as well.

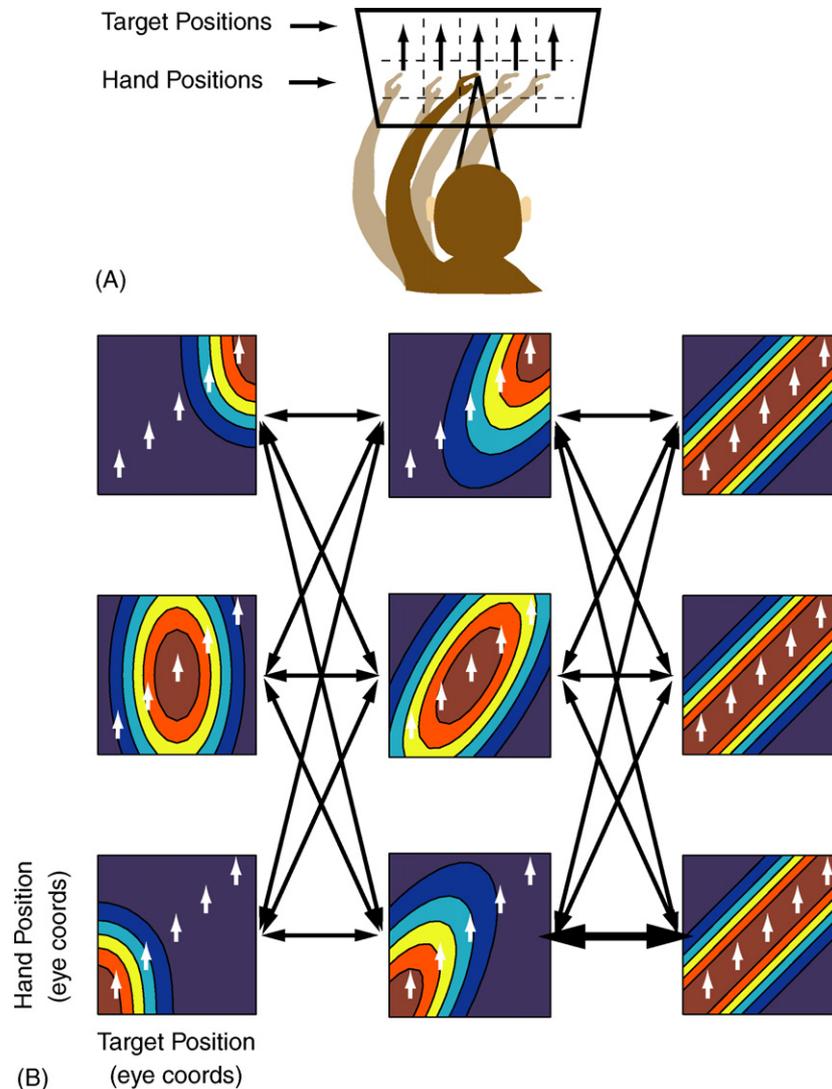


Fig. 3. (A) Example of an experiment in which a monkey makes reaching movements from each of five starting locations, to each of five target locations while fixating straight ahead. Reaches straight ‘up’ from each starting location are indicated by black arrows; reaches to other locations are not shown. (B) Responses of idealized PPC neurons. In each colomap, the firing rate of the neuron is plotted as a function of horizontal target position and vertical hand position; higher firing rates are indicated by redder hues. The white arrows indicate the movements shown in (A). The first column shows neurons that encode target position and hand position separately (Eq. (1)), in eye coordinates (i.e. eye-centered motor error). The last column shows neurons that encode target location inseparably (i.e. hand-centered motor error; Eq. (2)). The middle column shows neurons whose response is a function of motor error in both eye and hand coordinates.

explicit movement representations do appear to exist in the PPC and elsewhere, it is not necessary to have populations of neurons that encode motor error in this way; a distributed representation can in principle serve the same function (Andersen & Brotchie, 1992; Goodman & Andersen, 1989).

2. Spatial representations for reaching in the SPL

As stated above, motor error can and may be computed from either body-centered or eye-centered representations of target and hand position. For the past several years we have been conducting experiments aimed at uncovering the scheme that best accounts for the responses of SPL neurons during an instructed delay reaching task. We reasoned that if hand and/or target position are encoded in a particular frame of reference (say eye coordinates), then neural activity should not vary if these exper-

imental variables are held constant in that frame, but vary in other frames of reference (such as body or world coordinates). We also reasoned that if hand and target position are encoded separately in a particular frame, responses of individual neurons should resemble the two-dimensional gain fields shown in Fig. 3B (left column), while if they are encoded inseparably they should resemble the response fields in the rightmost column of this figure.

In terms of the manner in which hand and target position are encoded at the single cell level, we have generally found a continuum of responses in the SPL, from highly separable to highly inseparable. Three example neurons are shown in Fig. 4. As stated above, cells that appear to encode hand and target position inseparably can be described as coding motor error in hand-centered coordinates. The rightmost cell in Fig. 4 seems to fit this description well; this cell fired maximally

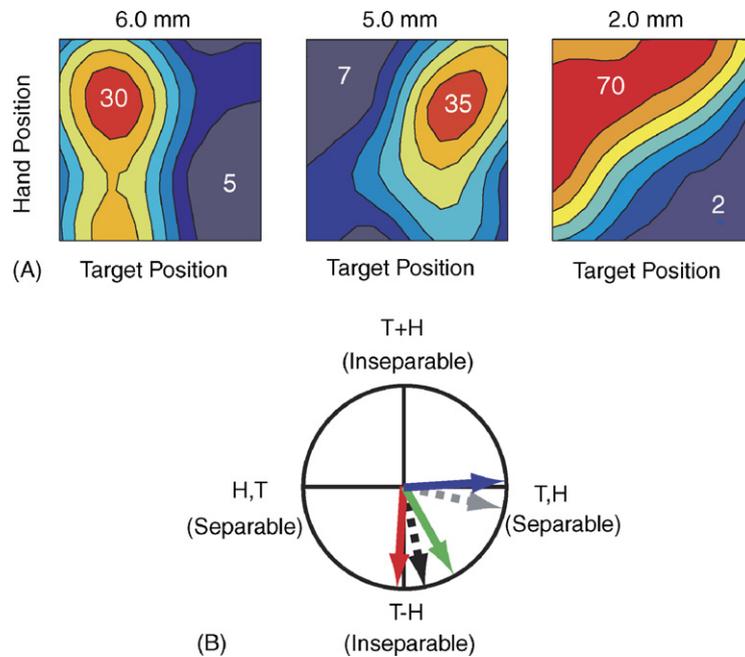


Fig. 4. (A) Responses of real PPC neurons in experiments similar to those shown in Fig. 3. In each colormap, the firing rate of the neuron during the memory period of an instructed delay task is plotted as a function of horizontal target position and horizontal hand position; higher firing rates are indicated by redder hues. Values superimposed on the colormaps represent mean firing rates in spikes/s. The value above each colormap indicates the depth (below dura) at which that neuron was recorded. (B) Vectorial representation of the degree of separability of neural responses to manipulations of target position and hand position, using the gradient method of Buneo, Jarvis, et al. (2002). The red, green, and blue vectors correspond to the neurons in (A) that were recorded at 2.0, 5.0, and 6.0 mm, respectively. The black vector represents the average degree of separability of 22 neurons recorded at depths 2.5 mm and above. The gray vector represents an average of 50 neurons recorded at depths below 2.5 mm.

for movements planned down and to the left of the starting position of the hand, for all positions of the hand in the visual field. Activity used to construct the response field of this cell, as well as the other cells in this figure, was derived from the planning period of an instructed delay task. During movement execution, the activity of hand-centered neurons is likely to encode more than just motor error; as emphasized by the work of Georgopoulos and colleagues, some combination of hand position and velocity may be represented as well (Ashe & Georgopoulos, 1994; Averbach, Chafee, Crowe, & Georgopoulos, 2005; Georgopoulos, Caminiti, & Kalaska, 1984; Georgopoulos & Massey, 1985). Interestingly, the activity of hand-centered neurons, as well as other PPC cell types described below, generally looks very similar during both the planning and execution periods of instructed delay tasks, at least with regard to reference frames, suggesting that planning and execution employ similar strategies for representing movement related variables in the PPC.

Fig. 4 also shows a cell from the PPC that appears to encode target and initial hand position separably (leftmost column). This single response field could be consistent with a coding of target and hand position in either body or eye-centered coordinates. However, when the responses of this and other separable cells are mapped for two different fixation positions, the responses are generally consistent with eye-centered rather than body-centered coordinates (Batista, Buneo, Snyder, & Andersen, 1999; Buneo & Andersen, 2003). Lastly, many neurons encountered in the SPL appeared neither inseparable or separable but possessed qualities of both encoding schemes (Buneo, Jarvis, et

al., 2002). An example is shown in the middle column of Fig. 4. Such cells resemble the idealized responses in the middle column of Fig. 3B, i.e. they have properties consistent with those of neurons in intermediate layers of artificial neural networks (Burnod et al., 1999; Deneve, Latham, & Pouget, 2001; Xing & Andersen, 2000; Zipser & Andersen, 1988) and as a result likely play the most critical role in the transformation between eye and hand-centered representations. In terms of reference frames, these cells can be considered to be encoding in both eye and hand coordinates.

The diversity of responses encountered in the SPL begs the question: is there any anatomical trend in the types of responses that are observed? To gain insight into this question, we characterized in one animal the degree of separability of target and hand position signals at the single cell level and related this to the distance from the cortical surface at which the cell was recorded. This analysis provided evidence for a ‘separability gradient’ with recording depth: cells that appeared to be coding the difference between target and hand position were more likely to be found close to the cortical surface (i.e. in area 5), while the more separable, eye-centered cells were generally found deeper in the sulcus, within PRR (Fig. 4). This trend is consistent with an earlier investigation of these two areas (Buneo, Jarvis, et al., 2002), and is also consistent with previous observations that ventral parts of the SPL (i.e. those in the medial bank of the intraparietal sulcus) show more prominent visual or ‘signal’ related activity than more dorsal regions (Caminiti et al., 1996; Colby & Duhamel, 1991; Graziano, Cooke, & Taylor, 2000; Kalaska, 1996; Kalaska & Crammond, 1995).

Thus, the responses of neurons in PRR and area 5 are well explained by a scheme that maps target locations and hand locations in eye coordinates to a corresponding motor error in hand coordinates. What is the nature of this mapping? It could be that the hand-centered neurons in area 5 result from a convergence of input from the gain-field like neurons found in PRR (Salinas & Abbott, 1995; Zipser & Andersen, 1988); in this way the mapping can be thought of as a vector subtraction of target and hand position signals, in eye coordinates, that is implemented gradually along the ventro–dorsal axis of the SPL, leading to single neurons that are progressively more hand-centered. A role for the PPC in vector subtraction has been suggested by other investigators as well, though without regard to a particular coordinate frame (Bullock, Cisek, & Grossberg, 1998; Desmurget et al., 1999). Alternatively, this mapping could represent an immediate convergence of eye-centered spatial information with corollary discharge from “downstream” motor areas that are recurrently connected to area 5 (Deneve et al., 2001), an idea that is perhaps more in line with the known anatomical connections to and from the SPL (Johnson, Ferraina, Bianchi, & Caminiti, 1996; Marconi et al., 2001). In either case, we can refer to the mapping between eye and hand coordinates as a *direct* transformation (Buneo, Jarvis, et al., 2002) in that it does not require target position to be transformed into intermediate head and body-centered reference frames, as would be required for schemes based on a subtraction of target and hand position in body-centered coordinates (Flanders, Helms-Tillery, & Soechting, 1992; Henriques, Klier, Smith, Lowy, & Crawford, 1998; McIntyre, Stratta, & Lacquaniti, 1998). In the following section, we discuss evidence from other labs that support the existence of such direct transformations. We also clarify certain aspects of this scheme and discuss its generality in arm movement planning and control.

2.1. Evidence in support of direct visuomotor transformations

In recent years, a number of behavioral studies in humans and studies of reach-related areas in the monkey have emphasized the primacy of eye-centered coordinates in movement planning. First, stimulation studies of the monkey superior colliculus (SC) suggest that this structure encodes gaze direction in retinal coordinates, rather than gaze displacement or gaze direction in space (Klier, Wang, & Crawford, 2001). Electrophysiological studies of the SC (Stuphorn, Bauswein, & Hoffman, 2000), ventral premotor cortex (Mushiake, Tanatsugu, & Tanji, 1997; Schwartz, Moran, & Reina, 2004), and dorsal premotor cortex (Shen & Alexander, 1997b), have identified populations of arm movement related neurons that are either clearly eye-centered or consistent with eye-centered coding and in some instances these neurons coexist with ones that appear arm or hand-centered. In the PPC, Cisek and Kalaska (2002) have shown that when animals are allowed to reach under free gaze conditions, the responses of neurons in the ‘medial parietal cortex’ (likely MIP) are still best understood as being eye or gaze-centered, consistent with the results of Batista et al. (1999).

Behaviorally speaking, vision has a profound effect upon arm movements, even soon after birth (Vandermeer, Vanderweel, &

Lee, 1995). These effects are perhaps best revealed in experiments where visual feedback of the hand is altered. Studies have shown that under such conditions subjects will alter the arms trajectory so the path *appears* visually straight, even if it is not (Wolpert, Ghahramani, & Jordan, 1995), and even when paths are displayed as a plot of elbow versus shoulder angle, i.e. in intrinsic coordinates (Flanagan & Rao, 1995). More recent studies provide evidence that this strong influence of vision on arm movements is related, at least in part, to an encoding of reach related variables in eye-centered coordinates. First, when reaching movements are performed to remembered targets in three-dimensional space with at least some visual feedback of the moving limb, the patterns of variable errors (McIntyre et al., 1997, 1998) and constant errors (Flanders et al., 1992) suggest a coordinate system centered on the line of sight. Patterns of generalization to local remappings between visual stimuli and fingertip position also appear consistent with an spherical eye-centered coordinate system (Vetter, Goodbody, & Wolpert, 1999). Updating of reach plans in eye-centered coordinates has been demonstrated psychophysically in humans (Henriques et al., 1998) and appears to be independent of the sensory modality used to cue the movement (Pouget, Ducom, Torri, & Bavelier, 2002). Moreover, imaging studies support a role for the PPC in the updating of reach plans (Medendorp, Goltz, Vilis, & Crawford, 2003), consistent with the findings of Batista et al. (1999). Lastly, a recent study of patients with optic ataxia, a disorder associated with damage to the PPC, showed that the reaching errors that characterize this disorder depend on the perceived position of the reach target, in eye coordinates, at the time of reaching (Khan et al., 2005).

3. Direct visuomotor transformations: expanding the hypothesis

3.1. Hand position in eye coordinates

A critical aspect of the direct transformation scheme is the coding of hand position in eye coordinates. However, from both a mathematical and intuitive standpoint, it is impossible to distinguish an encoding of hand position in eye coordinates from, say, an encoding of eye position in hand coordinates. In other words, a cell whose response could be described as coding target and hand position in eye coordinates:

$$fr = f(T_E) \times g(H_E) \quad (3)$$

where T_E is the target position in eye coordinates and H_E is the hand position in eye coordinates, would look indistinguishable from a neuron whose response could be described in the following way:

$$fr = f(T_E) \times g(E_H) \quad (4)$$

where E_H is eye position in hand coordinates. The reason for this is simple: the variables H_E and E_H are intrinsically indistinguishable. This can be appreciated from an examination of Fig. 2; switching from H_E to E_H involves merely inverting the sense of the depicted vector. Thus, both variables represent a

neural signal that encodes the *relative* position of the eyes and hand, and as a result, this signal does not have a single well-defined reference frame. Taking this idea to the extreme, one could also describe the variable T_E as reflecting not retinotopicity, but a code for eye position in a target-centered reference frame. This indeterminacy with regard to frames of reference is actually considered an advantage in multiple gain field or basis-function representations, i.e. since such representations do not employ a single reference frame they can be easily exploited for many different computations, including bi-directional transformations between representations with more clearly defined (or explicit) reference frames. Why then have we chosen to interpret PRR activity related to the relative positions of the eyes and hand as encoding hand position in eye coordinates? Our reason is the following: we hold that it is the required *computation* that determines the reference frame to which such signals should be attached. In PRR, reach targets are encoded in eye coordinates while in the adjacent area 5 they are encoded in both eye and hand coordinates or exclusively in hand coordinates (in the cells closest to the cortical surface). In this context, it makes sense to interpret activity related to the relative positions of the eyes and hand as encoding “hand position in eye coordinates”, as the sensorimotor transformations for reaching can then be described as a simple vector subtraction in eye coordinates, a scheme that is consistent with behavioral and lesion studies in human and non-human primates. In other areas of the brain, or simply in other contexts, this same activity may be interpreted differently. For example, this activity could be interpreted as “eye position in hand coordinates” in eye movement areas of the brain, particularly those that play a role in driving the eyes to the position of the unseen hand during eye-hand coordination tasks.

3.2. Generalizing to three dimensions

In the studies by Batista et al. (1999) and Buneo, Jarvis, et al. (2002), reaches were made between locations on a vertically oriented surface, thereby testing only for sensitivity to 2D retinal position. In order for the direct transformation scheme to be applicable to movements in three dimensions, PRR neurons should also be sensitive to target depth. This type of representation is found in LIP; here neurons are not only modulated by the location of objects on the retina but also by changes in binocular disparity and fixation distance (Genovesio & Ferraina, 2004; Gnadt & Mays, 1995). PRR neurons may use similar mechanisms to code target depth and experiments to test this hypothesis are currently underway.

3.3. Gain fields for eye, head, and arm position

The direct transformation scheme predicts that few if any neurons should have response fields for target position that are *explicitly* head or body-centered. This scheme however does not preclude the existence of eye and head position gain fields in the SPL. Modulation of responses by eye position, independent of retinal position, have been found in many areas of the brain, including those known to play a role in reach-

ing (Boussaoud & Bremmer, 1999; Salinas & Thier, 2000). Among these are areas 7a (Andersen, Bracewell, Barash, Gnadt, & Fogassi, 1990; Andersen, Essick, & Siegel, 1985; Andersen & Mountcastle, 1983), where eye position gain fields are combined with head-position signals (Brochic, Andersen, Snyder, & Goodman, 1995), and V6A of the PPC (Battaglia-Mayer et al., 2000; Galletti, Battaglini, & Fattori, 1995; Nakamura, Chung, Graziano, & Gross, 1999). Modulation of reach-related activity by eye position has even been reported in the dorsal premotor cortex (Boussaoud, Jouffrais, & Bremmer, 1998), though the precise magnitude of these effects may vary under different behavioral conditions (Cisek & Kalaska, 2002).

It was initially proposed that the convergence of retinal and eye position signals in area 7a served to provide a distributed representation of target location in head-centered coordinates (Andersen et al., 1985). Such a representation would be useful for motor structures involved in the control of gaze. Subsequent studies showed however that although both area 7a and LIP are modulated by head position (Brochic et al., 1995), consistent with a role for these areas in planning gaze shifts, this modulation appears to be driven largely by vestibular input in area 7a, arguing for a distributed, world-centered representation in this area that may be useful for navigation (Snyder, Grieve, Brochic, & Andersen, 1998). In contrast, head position modulation in LIP appears to be driven largely by proprioceptive signals and/or efference copy from the head/neck motor system, leading to the distributed body-centered representation that is more useful for the control of gaze shifts (Snyder, Grieve, et al., 1998).

These results raise the following question: if reach target locations are transformed directly from eye to hand-centered coordinates in the SPL, what purpose would these gain fields serve in the reach pathway? First, as pointed out by Crawford and colleagues, a scheme which fails to account for the fact that vector displacements are coordinate frame dependent would result in consistent mislocalization of targets (Crawford & Guitton, 1997; Crawford et al., 2004). Psychophysical experiments have shown that such factors are taken into account by the motor system (Crawford, Henriques, & Vilis, 2000) and eye and head position gain fields likely play a role in this process. Second, only an intrinsic representation of motor error, i.e. one expressed in terms of changes in arm configuration, can be used as an input to structures concerned with dynamics (Flanders, Hondzinski, Soechting, & Jackson, 2003). Thus, a mechanism must exist for converting hand-centered motor error into an intrinsic motor error and gain fields for eye, head and arm configuration may represent one aspect of this mechanism. Lastly, these same signals could be used in the reverse process as well, i.e. in transforming a representation of hand position based on proprioceptive signals and efference copy of arm movement commands, into the eye-centered representation of hand position that is found in PRR (Buneo & Andersen, 2003; Shadmehr & Wise, 2005).

Consistent with these ideas, a number of studies have demonstrated that gaze signals, independent of retinal position, play an important role in the reach system. For example, reaches are more accurate when the eyes are directed at reach targets than when they are directed away from them (Bock, 1986, 1993), even

when these targets are not concurrently visible (Enright, 1995). Moreover, when human subjects are required to track visual targets in the presence of an illusion that distorts perceived target motion, errors in pointing are strongly correlated with errors in gaze position (Soechting, Engel, & Flanders, 2001). Studies in non-human primates suggest that it is efference copy of eye movement commands, rather than extraocular muscle proprioception, that provides the gaze signals used to assist the hand in reaching the target (Lewis, Gaymard, & Tamargo, 1998).

How does the integration of motor error and body position (eye, head, etc.) signals manifest in the reach pathways of the brain? One possibility is that there are separate populations in the PPC devoted to the encoding of body position signals and motor error. These separate signals could then converge on single neurons in the frontal lobe to achieve the required integration. Another possibility is that motor error and body position signals are multiplexed within the PPC, and then transmitted to the frontal lobe. In consonance with this latter idea, preliminary results obtained from ventral regions of the SPL suggest that single neurons in this area do integrate eye position signals with information about target and hand position in eye coordinates (Buneo & Andersen, 2002), though it is presently unclear whether head position signals are multiplexed in the same way.

It seems appropriate at this point to discuss the ramifications of the direct transformation scheme for frontal lobe function. The reason for this is simple: it is well established that the frontal and parietal reach areas are extensively interconnected, with areas located more posteriorly in the parietal cortex (e.g. V6A) being linked more strongly to anterior frontal areas such as rostral premotor cortex, and more anteriorly located parietal areas (PE/dorsal area 5) being linked to more caudal frontal areas such as M1 (Marconi et al., 2001). Importantly, this “neuroanatomical gradient” appears to parallel a gradient in the functional properties of neurons in the frontal and parietal lobes, and it has been suggested that the neuroanatomical gradient serves to connect functionally similar neurons in the parietal lobe with their counterparts in the frontal lobe (Caminiti et al., 1996; Johnson et al., 1996). Thus, with regard to frames of reference and coordinates systems, the finding of a gradual transition from purely eye-centered to a purely hand or arm-centered representation in the parietal lobe appears to suggest that one should find a similar transition somewhere within the frontal lobe. Interestingly, several recent studies have pointed to a greater influence of extrinsic reference frames in reach-related neurons of the both the dorsal and ventral premotor cortex than in M1 (Kakei, Hoffman, & Strick, 1999, 2001; Mushiaki et al., 1997; Schwartz et al., 2004; Shen & Alexander, 1997a,b). Similarly, other studies report a gradient of sensitivity to eye position signals along the rostro-caudal extent of dorsal premotor cortex (Boussaoud et al., 1998; Fujii, Mushiaki, & Tanji, 2000), though as stated previously the magnitude of these effects may vary under different behavioral conditions (Cisek & Kalaska, 2002). In short, although the above findings do not directly support the existence of an eye to limb centered representation within the frontal lobe they are suggestive of the phenomenon, and experiments to test the hypothesis directly are currently underway.

3.4. Motor error: intrinsic or extrinsic?

Thus, far we have assumed that motor error is defined in extrinsic or hand-centered space within the PPC. However, as pointed out earlier, this signal would be inadequate as an input to the control centers for reaching, which must contend with substantial variations in the mechanical properties of the arm as a function of its configuration (Buneo, Soechting, & Flanders, 1997, 2002; Soechting et al., 1995). It is generally assumed that accounting for such ‘intrinsic’ factors is the domain of the frontal lobe. In support of this idea, the activity of neurons in the premotor and motor cortex during step-tracking movements of the wrist appear to be consistent with a role for these structures in converting extrinsic motor error into the requisite muscle activation patterns required to realize the movement (Kakei et al., 1999, 2001). However, there is evidence suggesting that neurons in area 5 of the PPC are also influenced by intrinsic factors (Ferraina & Bianchi, 1994; Lacquaniti, Guigon, Bianchi, Ferraina, & Caminiti, 1995; Scott, Sergio, & Kalaska, 1997), though it is presently unclear whether the changes in cell activity that have been reported are indicative of an explicit encoding of motor error in intrinsic coordinates, or a hybrid representation signaling extrinsic motor error and arm configuration (that could be used to derive intrinsic motor error). If motor error *is* defined in intrinsic coordinates in parts of the SPL, it would imply that the PPC maps three-dimensional target and hand positions in eye-centered coordinates to the four-dimensional space of arm postures (ignoring motion of hand and wrist). This could provide a basis for the observation that adaptation to a novel visuomotor mapping depends on the starting arm configuration (Baraduc & Wolpert, 2002). It would also suggest that embedded within the direct transformation scheme is a solution to the problem of kinematic redundancy, though it would not by itself indicate the nature of this solution. The aforementioned head and eye position “gain fields”, as well as signals encoding the position and orientation of the arm would likely play an important role in such a solution.

3.5. Dynamics

Dynamics refers to the forces and torques that produce motion. The observation that area 5 activity varies with changes in arm configuration does not necessarily mean that area 5 is directly involved in computing the joint torques or muscle forces that produce motion of the arm. In fact, it has been reported that area 5 cells are relatively insensitive to the application of external loads, both during the maintenance of static postures and during movement (Kalaska, Cohen, Prudhomme, & Hyde, 1990). This could mean that area 5 occupies an intermediate stage between sensation and movement that is intrinsic in nature but dynamics free (Torres & Zipser, 2002). However, it has recently been shown that transcranial magnetic stimulation (TMS) of the PPC impairs the learning of novel arm dynamics (Della-Maggiore, Malfait, Ostry, & Paus, 2004), suggesting that at least in humans this area is concerned to some degree with dynamics. Perhaps the issue is not whether the PPC is sensitive to dynamics, but the manner in which it is sensitive. In certain contexts, an area

could be expected to be sensitive to changing dynamics, without being explicitly involved in computing the dynamics required to generate a movement. One such scenario is discussed in the next section.

4. The PPC, online control, and forward models

In the experiments of Batista et al. (1999), Buneo, Jarvis, et al. (2002), movements were performed ‘open loop’ with respect to visual feedback. However, reaching movements are generally made under visually closed-loop conditions. Could a direct transformation scheme work for such movements? Psychophysical studies in humans have clearly pointed to a role for the PPC in the rapid online updating of movements (Desmurget et al., 1999; Pisella et al., 2000). However, in order for the direct transformation scheme to play a significant role in this process would require that estimation of hand position, in eye coordinates, be dependent upon mechanisms other than visual feedback, which is generally considered to be too slow to accomplish the task (Desmurget & Grafton, 2000). In other words, the estimation of hand position would have to reflect the participation of a forward model, that is, a system that combines efference copy of ongoing motor commands, sensory feedback (visual and somatosensory) and an internal model of the dynamics of the arm, to estimate the current state (position, velocity, etc.) of the limb (Jordan & Rumelhart, 1992; Kawato, 1999). Evidence in support of this idea comes from studies of human subjects that are required to track the position of the unseen arm after it has been unpredictably perturbed (Ariff, Donchin, Nanayakkara, & Shadmehr, 2002; Nanayakkara & Shadmehr, 2003). In these studies, the endpoints of post perturbation saccades predicted the future position of the hand, but only when the dynamics of the arm were predictable. These results were interpreted as evidence that the brain continually computes an estimate of current hand position, in *eye* coordinates, based on a forward model. Moreover, damage to the SPL can lead to deficits that are consistent with an inability to maintain internal estimates of arm state, including a difficulty in maintaining constant force output in the absence of vision (Wolpert, Goodbody, & Husain, 1998), suggesting that the SPL plays an important role in computing the aforementioned estimate of hand state. In summary, human behavioral evidence supports the idea that a form of direct transformation scheme, one that makes use of a forward model to estimate the position of the hand in eye coordinates, can conceivably support the rapid, online control of visually guided arm movements.

Forward models can be used not only to estimate current arm state, but the future state of the arm as well. It is tempting to speculate that the tuning for target position observed in the studies of Batista et al. (1999) reflects not only the intended reach but also an estimate, as a consequence of this intention, of the position of the arm in eye coordinates at some point in the future. There is some experimental support for this idea. For example, it is known that cells in LIP exhibit predictive updating, i.e. they begin to fire merely in expectation of the appearance of a saccade target in their receptive field, suggesting that LIP may have access to an estimate of the future position of the eyes (Duhamel, Colby, & Goldberg, 1992; Gnadt

& Andersen, 1988; Kusunoki & Goldberg, 2003; Mazzone et al., 1996). Although target-related activity in PRR updates, in eye coordinates, in response to changes in eye position (Batista et al., 1999), no evidence of *predictive* updating of either target or hand position has yet been observed. On the other hand, several lines of evidence suggest that target-related activity in the SPL is not simply a visual memory response. Target related activity is specific for planned reaches and not planned saccades (Snyder et al., 1997; Snyder, Batista, et al., 1998), can be elicited by either visual or auditory stimuli (Cohen & Andersen, 2000), and when multiple targets are presented in a sequence, reflects only the next planned movement (Batista & Andersen, 2001). Moreover, tasks employing anti-reach paradigms generally report that SPL activity reflects the direction of planned movement and not the location of the stimuli that cues that movement (Eskandar & Assad, 1999; Kalaska & Crammond, 1995). One difficulty with interpreting target related activity in the PPC as a future state estimate is the observation that area 5 activity persists in ‘no-go’ trials (Kalaska, 1996; Kalaska & Crammond, 1995); it is unclear what purpose a state estimate would serve when no movement is to be executed. However, this activity could simply represent a default intention/estimate that persists in the PPC until another one takes its place (Andersen & Buneo, 2002; Bracewell et al., 1996; Snyder, Batista, et al., 1998).

5. Context-dependent visuomotor transformations

Although the notion of a direct transformation scheme makes intuitive sense and is supported by human psychophysical and monkey neurophysiological studies, it is unlikely that a single scheme can be used in all contexts. Another transformation scheme that has been put forth involves the progressive transformation of target information from retinal to head and ultimately body-centered coordinates. Motor error is then computed by comparing a body-centered representation of target position with a body-centered representation of hand position that is derived largely from proprioception and efference copy. This scheme might be used to generate reaches in contexts where a more direct scheme would be impractical, e.g. when visual information about the location of the target and/or hand is unreliable or unavailable (Engel, Flanders, & Soechting, 2002). As stated earlier, when reaching movements are performed to remembered target locations with at least some visual feedback of the moving limb, the patterns of variable errors (McIntyre et al., 1997, 1998) and constant errors (Flanders et al., 1992) suggest a coordinate system centered on the sight-line. However, when movements are made to remembered locations in the dark, a different pattern emerges. Constant errors suggest a coordinate system centered on the shoulder of the pointing arm (Flanders et al., 1992). Similarly, variable errors, particularly following long delays in darkness, suggest a transformation scheme that depends on starting position of the effector with respect to the body (McIntyre et al., 1998). Interestingly, when movements are made without delay to continuously viewed targets and without concurrent vision of the moving limb, patterns of variable errors appear strikingly similar to those obtained at long delays in the

dark (Carrozzo, McIntyre, Zago, & Lacquaniti, 1999). These results could point to a context-dependent shift in visuomotor transformation schemes (Engel et al., 2002; Heuer & Sangals, 1998; Sober & Sabes, 2005), with this shift being gated perhaps by the degree and reliability of visual information from the moving limb.

Another way in which visuomotor transformation schemes could be context-dependent is with regard to the notion of ‘automatic’ and ‘slow’ modes of control. Comparative studies of neurologically normal humans and patients with optic ataxia suggest that the SPL may be preferentially involved in the planning and control of a particular type of action: rapid or “automatically” generated movements performed under visual guidance (Desmurget et al., 1999; Pisella et al., 2000). Patients with optic ataxia exhibit marked difficulty in making corrections to their ongoing arm movements in response to a sudden change in the location of a reaching target, suggesting an impairment in the system responsible for rapid updating of movements. Importantly, these patients can correct their ongoing movements; they just do so in a slower and more deliberate fashion than their neurologically intact counterparts. These observations have led to the proposal that there are two distinct brain systems for the control of visually guided action: a fast-acting “automatic” system and a slower “cognitive” one that would augment or even substitute for the automatic one under certain conditions. It is tempting to speculate that these two systems are subserved by different visuomotor transformation schemes, e.g. the fast SPL based automatic system by a direct scheme and the slower cognitive system by a scheme that is more indirect. Some experimental evidence exists in support of such an idea (Rossetti & Pisella, 2002). Thus, it is possible that reaching under visual guidance could in most circumstances be thought of as reflecting the interaction of two (or more) visuomotor transformation schemes, even perhaps during different phases of a single movement (initiation versus terminus).

6. Conclusion

In this review, we have presented evidence in support of the idea that the PPC acts as a sensorimotor interface for visually guided eye and arm movements. In the brain, and in particular within the PPC, this interface takes the form of a mapping, and in the context of arm movements, this mapping appears to be between representations of target and hand position in eye coordinates, and a representation of motor error in hand-centered coordinates. The mapping is ‘direct’ in the sense that it does not require information about target position to be transformed into intermediate head and body-centered reference frames in order to compute motor error, but manifests in the PPC as a gradual change in the functional properties of cells along the ventro–dorsal axis of the SPL, i.e. from deep in the sulcus to the cortical surface (Fig. 4). This scheme is illustrated schematically in Fig. 1 and again in Fig. 5, which also shows ‘later’ stages in the planning of point-to-point reaches. Although psychophysical, neurophysiological and simulation studies reviewed here support the idea of direct transformations and the PPC’s role in them, many unanswered questions remain regarding the PPC’s role in these later planning stages. For example, does the PPC play a role in transforming a hand-centered motor error signal into a desired change in joint angles, and in determining the forces required to move the arm, or are these computations the domain of the frontal lobe? What role do eye, head, and arm position gain fields play in these computations and at what stage or stages are they combined with representations of target position, hand position and motor error? Answers to such questions are critical not only to our understanding of the PPC but also to our understanding of the relative roles of the parietal and frontal cortices in visually guided reaching.

It is also unclear at this time precisely how involved the PPC is in state estimation and the online control of visually guided arm movements. Studies of neurologically intact subjects as well

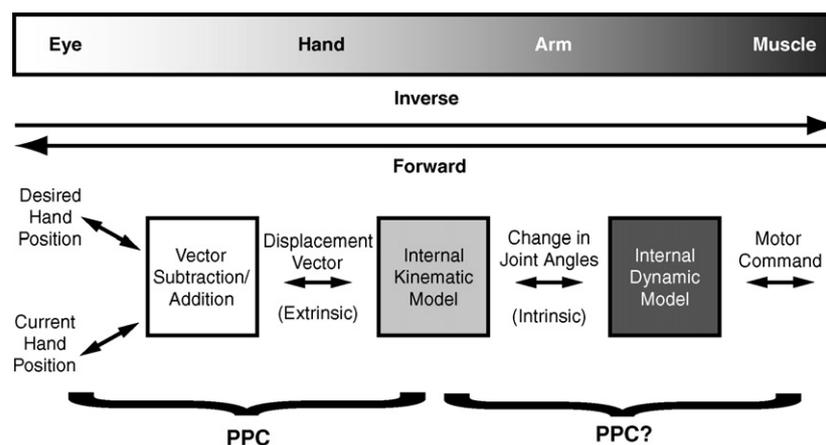


Fig. 5. Schematic of the operations involved in planning reaches, as well as the PPC’s presumed role in these operations. Additional signals are required to transform between some of the depicted representations, e.g. information regarding the position/configuration of the eyes, head, and arm derived from efference copy and/or proprioception, but for simplicity are not shown. Note that all operations are depicted as being recurrent in order to reflect the convergence of recent anatomical, physiological, behavioral and simulation data regarding this issue (Buneo, Jarvis, et al., 2002; Burnod et al., 1999; Caminiti et al., 1996; Deneve et al., 2001; Marconi et al., 2001; Pouget et al., 2002; Shadmehr & Wise, 2005). It should also be noted that although the diagram implies that the same networks of neurons are involved in both the forward and inverse computations, it is currently unclear whether this is or is not the case.

as patients generally support the idea, at least in the context of rapid movements performed under visual guidance (Desmurget et al., 1999; Pisella et al., 2000). Human studies also point to a role for the PPC in estimating the current state of the limb based on a forward model (Wolpert et al., 1998), a presumed prerequisite for effective control, and other studies suggest this estimate is encoded in eye-centered coordinates (Ariff et al., 2002; Nanayakkara & Shadmehr, 2003), in apparent agreement with neurophysiological studies of the PPC (Buneo, Jarvis, et al., 2002). More direct neurophysiological evidence for a role in state estimation and online control is needed, however. One tractable question in this regard concerns the eye-centered representation of hand position in the PPC; if this representation can be shown to persist in the absence of vision, it would suggest the representation is derived from transformed somatosensory information/and or efference copy of a previously issued motor command. This would support the idea that the PPC plays a role in constructing a supramodal estimate of arm state, in eye coordinates, that would be advantageous for functions such as online control. Experiments designed to answer this and other questions are currently underway and should advance not only our understanding of the PPC and its place in the perception-action cycle but also contribute to the development of more advanced theoretical and computational models of arm movement planning and control.

Acknowledgments

We wish to thank the generous support of the James G. Boswell Foundation, the Sloan-Swartz Center for Theoretical Neurobiology, the National Eye Institute (NEI), the Defense Advanced Research Projects Agency (DARPA), the Office of Naval Research (ONR), and the Christopher Reeves Foundation. We also thank Bijan Pesaran, Aaron Batista and Murray Jarvis for helpful discussions.

References

- Andersen, R. A., Bracewell, R. M., Barash, S., Gnadt, J. W., & Fogassi, L. (1990). Eye position effects on visual, memory, and saccade-related activity in areas LIP and 7a of macaque. *The Journal of Neuroscience*, *10*(4), 1176–1196.
- Andersen, R. A., & Brotchie, P. R. (1992). Spatial maps versus distributed representations and a role for attention. *Behavioral and Brain Sciences*, *15*(4), 707–709.
- Andersen, R. A., & Buneo, C. A. (2002). Intentional maps in posterior parietal cortex. *Annual Review of Neuroscience*, *25*, 189–220.
- Andersen, R. A., Essick, G. K., & Siegel, R. M. (1985). Encoding of spatial location by posterior parietal neurons. *Science*, *25*, 456–458.
- Andersen, R. A., Essick, G. K., & Siegel, R. M. (1987). Neurons of area 7a activated by both visual stimuli and oculomotor behavior. *Experimental Brain Research*, *67*, 316–322.
- Andersen, R. A., & Mountcastle, V. B. (1983). The influence of the angle of gaze upon the excitability of the light-sensitive neurons of the posterior parietal cortex. *The Journal of Neuroscience*, *3*(3), 532–548.
- Ariff, G., Donchin, O., Nanayakkara, T., & Shadmehr, R. (2002). A real-time state predictor in motor control: Study of saccadic eye movements during unseen reaching movements. *Journal of Neuroscience*, *22*(17), 7721–7729.
- Ashe, J., & Georgopoulos, A. P. (1994). Movement parameters and neural activity in motor cortex and area-5. *Cerebral Cortex*, *4*(6), 590–600.
- Averbeck, B. B., Chafee, M. V., Crowe, D. A., & Georgopoulos, A. P. (2005). Parietal representation of hand velocity in a copy task. *Journal of Neurophysiology*, *93*(1), 508–518.
- Baraduc, P., & Wolpert, D. M. (2002). Adaptation to a visuomotor shift depends on the starting posture. *Journal of Neurophysiology*, *88*(2), 973–981.
- Batista, A. P., & Andersen, R. A. (2001). The parietal reach region codes the next planned movement in a sequential reach task. *Journal of Neurophysiology*, *85*(2), 539–544.
- Batista, A. P., Buneo, C. A., Snyder, L. H., & Andersen, R. A. (1999). Reach plans in eye-centered coordinates. *Science*, *285*, 257–260.
- Battaglia-Mayer, A., Ferraina, S., Marconi, B., Bullis, J. B., Lacquaniti, F., Burnod, Y., et al. (1998). Early motor influences on visuomotor transformations for reaching: A positive image of optic ataxia. *Experimental Brain Research*, *123*(1–2), 172–189.
- Battaglia-Mayer, A., Ferraina, S., Mitsuda, T., Marconi, B., Genovesio, A., Onorati, P., et al. (2000). Early coding of reaching in the parietooccipital cortex. *Journal of Neurophysiology*, *83*(4), 2374–2391.
- Bisley, J. W., & Goldberg, M. E. (2003). Neuronal activity in the lateral intraparietal area and spatial attention. *Science*, *299*(5603), 81–86.
- Bock, O. (1986). Contribution of retinal versus extraretinal signals towards visual localization in goal-directed movements. *Experimental Brain Research*, *64*(3), 476–482.
- Bock, O. (1993). Localization of objects in the peripheral visual-field. *Behavioural Brain Research*, *56*(1), 77–84.
- Boussaoud, D., & Bremmer, F. (1999). Gaze effects in the cerebral cortex: Reference frames for space coding and action. *Experimental Brain Research*, *128*(1–2), 170–180.
- Boussaoud, D., Joffrais, C., & Bremmer, F. (1998). Eye position effects on the neuronal activity of dorsal premotor cortex in the macaque monkey. *Journal of Neurophysiology*, *80*(3), 1132–1150.
- Bracewell, R. M., Mazzoni, P., Barash, S., & Andersen, R. A. (1996). Motor intention activity in the macaque's lateral intraparietal area. II. Changes of motor plan. *Journal of Neurophysiology*, *76*(3), 1457–1464.
- Brotchie, P. R., Andersen, R. A., Snyder, L. H., & Goodman, S. J. (1995). Head position signals used by parietal neurons to encode locations of visual stimuli. *Nature*, *375*(6528), 232–235.
- Bullock, D., Cisek, P., & Grossberg, S. (1998). Cortical networks for control of voluntary arm movements under variable force conditions. *Cerebral Cortex*, *8*(1), 48–62.
- Buneo, C. A., & Andersen, R. A. (2002). *Effects of gaze angle and vision of the hand on reach-related activity in the posterior parietal cortex*. Paper Presented at the Program No. 62.3. 2002 Abstract Viewer/Itinerary Planner, Washington, DC.
- Buneo, C. A., & Andersen, R. A. (2003). *The role of area 5 somatosensory input in visuomotor transformations for reaching*. Paper Presented at the Program No. 14.1. 2003 Abstract Viewer/Itinerary Planner, Washington DC.
- Buneo, C. A., Jarvis, M. R., Batista, A. P., & Andersen, R. A. (2002). Direct visuomotor transformations for reaching. *Nature*, *416*(6881), 632–636.
- Buneo, C. A., Soechting, J. F., & Flanders, M. (1997). Postural dependence of muscle actions: Implications for neural control. *Journal of Neuroscience*, *17*(6), 2128–2142.
- Buneo, C. A., Soechting, J. F., & Flanders, M. (2002). Capturing the frame of reference of shoulder muscle forces. *Archives Italiennes De Biologie*, *140*(3), 237–245.
- Burnod, Y., Baraduc, P., Battaglia-Mayer, A., Guigon, E., Koehlin, E., Ferraina, S., et al. (1999). Parieto-frontal coding of reaching: An integrated framework. *Experimental Brain Research*, *129*(3), 325–346.
- Calton, J. L., Dickinson, A. R., & Snyder, L. H. (2002). Non-spatial, motor-specific activation in posterior parietal cortex. *Nature Neuroscience*, *5*(6), 580–588.
- Caminiti, R., Ferraina, S., & Johnson, P. B. (1996). The sources of visual information to the primate frontal lobe: A novel role for the superior parietal lobule. *Cerebral Cortex*, *6*, 319–328.
- Carrozzo, M., McIntyre, J., Zago, M., & Lacquaniti, F. (1999). Viewer-centered and body-centered frames of reference in direct visuomotor transformations. *Experimental Brain Research*, *129*, 201–210.

- Cisek, P., & Kalaska, J. F. (2002). Modest gaze-related discharge modulation in monkey dorsal premotor cortex during a reaching task performed with free fixation. *Journal of Neurophysiology*, 88, 1064–1072.
- Clower, D. M., Hoffman, J. M., Votaw, J. R., Faber, T. L., Woods, R. P., & Alexander, G. E. (1996). Role of posterior parietal cortex in the recalibration of visually guided reaching. *Nature*, 383(6601), 618–621.
- Cohen, Y. E., & Andersen, R. A. (2000). Reaches to sounds encoded in an eye-centered reference frame. *Neuron*, 27(3), 647–652.
- Colby, C. L., & Duhamel, J. R. (1991). Heterogeneity of extrastriate visual areas and multiple parietal areas in the macaque monkey. *Neuropsychologia*, 29(6), 517–537.
- Colby, C. L., & Goldberg, M. E. (1999). Space and attention in parietal cortex. *Annual Review on Neuroscience*, 22, 319–349.
- Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., et al. (1998). A common network of functional areas for attention and eye movements. *Neuron*, 21(4), 761–773.
- Crawford, J. D., & Guitton, D. (1997). Visual-motor transformations required for accurate and kinematically correct saccades. *Journal of Neurophysiology*, 78(3), 1447–1467.
- Crawford, J. D., Henriques, D. Y. P., & Vilis, T. (2000). Curvature of visual space under vertical eye rotation: Implications for spatial vision and visuomotor control. *Journal of Neuroscience*, 20(6), 2360–2368.
- Crawford, J. D., Medendorp, W. P., & Marotta, J. J. (2004). Spatial transformations for eye-hand coordination. *Journal of Neurophysiology*, 92(1), 10–19.
- Della-Maggiore, V., Malfait, N., Ostry, D. J., & Paus, T. (2004). Stimulation of the posterior parietal cortex interferes with arm trajectory adjustments during the learning of new dynamics. *Journal of Neuroscience*, 24(44), 9971–9976.
- Deneve, S., Latham, P. E., & Pouget, A. (2001). Efficient computation and cue integration with noisy population codes. *Nature Neuroscience*, 4(8), 826–831.
- Desmurget, M., Epstein, C. M., Turner, R. S., Prablanc, C., Alexander, G. E., & Grafton, S. T. (1999). Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nature Neuroscience*, 2(6), 563–567.
- Desmurget, M., & Grafton, S. (2000). Forward modeling allows feedback control for fast reaching movements. *Trends in Cognitive Sciences*, 4(11), 423–431.
- Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, 255, 90–92.
- Engel, K. C., Flanders, M., & Soechting, J. F. (2002). Oculocentric frames of reference for limb movement. *Archives Italiennes De Biologie*, 140(3), 211–219.
- Enright, J. T. (1995). The nonvisual impact of eye orientation on eye-hand coordination. *Vision Research*, 35(11), 1611–1618.
- Eskandar, E. N., & Assad, J. A. (1999). Dissociation of visual, motor and predictive signals in parietal cortex during visual guidance. *Nature Neuroscience*, 2(1), 88–93.
- Ferraina, S., & Bianchi, L. (1994). Posterior parietal cortex—functional-properties of neurons in area-5 during an instructed-delay reaching task within different parts of space. *Experimental Brain Research*, 99(1), 175–178.
- Flanagan, J. R., & Rao, A. K. (1995). Trajectory adaptation to a nonlinear visuomotor transformation—evidence of motion planning in visually perceived space. *Journal of Neurophysiology*, 74(5), 2174–2178.
- Flanders, M., Helms-Tillery, S. I., & Soechting, J. F. (1992). Early stages in a sensorimotor transformation. *Behavioral and Brain Sciences*, 15, 309–362.
- Flanders, M., Hondzinski, J. M., Soechting, J. F., & Jackson, J. C. (2003). Using arm configuration to learn the effects of gyroscopes and other devices. *Journal of Neurophysiology*, 89(1), 450–459.
- Fujii, N., Mushiike, H., & Tanji, J. (2000). Rostrocaudal distinction of the dorsal premotor area based on oculomotor involvement. *Journal of Neurophysiology*, 83(3), 1764–1769.
- Galletti, C., Battaglini, P. P., & Fattori, P. (1995). Eye position influence on the parieto-occipital area PO (V6) of the macaque monkey. *The European Journal of Neuroscience*, 7(12), 2486–2501.
- Genovesio, A., & Ferraina, S. (2004). Integration of retinal disparity and fixation-distance related signals toward an egocentric coding of distance in the posterior parietal cortex of primates. *Journal of Neurophysiology*, 91(6), 2670–2684.
- Georgopoulos, A. P., Caminiti, R., & Kalaska, J. F. (1984). Static spatial effects in motor cortex and area 5: Quantitative relations in a two-dimensional space. *Experimental Brain Research*, 54(3), 446–454.
- Georgopoulos, A. P., & Massey, J. T. (1985). Static versus dynamic effects in motor cortex and area-5—comparison during movement time. *Behavioural Brain Research*, 18(2), 159–166.
- Gnadt, J. W., & Andersen, R. A. (1988). Memory related motor planning activity in posterior parietal cortex of macaque. *Experimental Brain Research*, 70, 216–220.
- Gnadt, J. W., & Mays, L. E. (1995). Neurons in monkey parietal area LIP are tuned for eye-movement parameters in three-dimensional space. *Journal of Neurophysiology*, 73(1), 280–297.
- Goodman, S. J., & Andersen, R. A. (1989). Microstimulation of a neural-network model for visually guided saccades. *Journal of Cognitive Neuroscience*, 1, 317–326.
- Gottlieb, J., & Goldberg, M. E. (1999). Activity of neurons in the lateral intraparietal area of the monkey during an antisaccade task. *Nature Neuroscience*, 2(10), 906–912.
- Gottlieb, J. P., Kusunoki, M., & Goldberg, M. E. (1998). The representation of visual salience in monkey parietal cortex. *Nature*, 391(6666), 481–484.
- Graziano, M. S., Cooke, D. F., & Taylor, C. S. (2000). Coding the location of the arm by sight. *Science*, 290(5497), 1782–1786.
- Henriques, D. Y., Klier, E. M., Smith, M. A., Lowy, D., & Crawford, J. D. (1998). Gaze-centered remapping of remembered visual space in an open-loop pointing task. *The Journal of Neuroscience*, 18(4), 1583–1594.
- Heuer, H., & Sangals, J. (1998). Task-dependent mixtures of coordinate systems in visuomotor transformations. *Experimental Brain Research*, 119(2), 224–236.
- Johnson, P. B., Ferraina, S., Bianchi, L., & Caminiti, R. (1996). Cortical networks for visual reaching: Physiological and anatomical organization of frontal and parietal lobe arm regions. *Cerebral Cortex*, 6(2), 102–119.
- Jordan, M. I., & Rumelhart, D. E. (1992). Forward models—supervised learning with a distal teacher. *Cognitive Science*, 16(3), 307–354.
- Kakei, S., Hoffman, D. S., & Strick, P. L. (1999). Muscle and movement representations in the primary motor cortex. *Science*, 285(5436), 2136–2139.
- Kakei, S., Hoffman, D. S., & Strick, P. L. (2001). Direction of action is represented in the ventral premotor cortex. *Nature Neuroscience*, 4(10), 1020–1025.
- Kalaska, J. F. (1996). Parietal cortex area 5 and visuomotor behavior. *Canadian Journal of Physiology and Pharmacology*, 74(4), 483–498.
- Kalaska, J. F., Cohen, D. A. D., Prudhomme, M., & Hyde, M. L. (1990). Parietal area-5 neuronal-activity encodes movement kinematics, not movement dynamics. *Experimental Brain Research*, 80(2), 351–364.
- Kalaska, J. F., & Crammond, D. J. (1995). Deciding not to GO: Neural correlates of response selection in a GO/NOGO task in primate premotor and parietal cortex. *Cerebral Cortex*, 5, 410–428.
- Kawato, M. (1999). Internal models for motor control and trajectory planning. *Current Opinion in Neurobiology*, 9(6), 718–727.
- Khan, A. Z., Pisella, L., Vighetto, A., Cotton, F., Luaute, J., Boisson, D., et al. (2005). Optic ataxia errors depend on remapped, not viewed, target location. *Nature Neuroscience*, 8(4), 418–420.
- Klier, E. M., Wang, H., & Crawford, J. D. (2001). The superior colliculus encodes gaze commands in retinal coordinates. *Nature Neuroscience*, 4, 627–632.
- Kustov, A. A., & Robinson, D. L. (1996). Shared neural control of attentional shifts and eye movements. *Nature*, 384(6604), 74–77.
- Kusunoki, M., & Goldberg, M. E. (2003). The time course of perisaccadic receptive field shifts in the lateral intraparietal area of the monkey. *Journal of Neurophysiology*, 89(3), 1519–1527.
- Lacquaniti, F., Guigon, E., Bianchi, L., Ferraina, S., & Caminiti, R. (1995). Representing spatial information for limb movement: Role of area 5 in the monkey. *Cerebral Cortex*, 5(5), 391–409.
- Lewis, R. F., Gaymard, B. M., & Tamargo, R. J. (1998). Efference copy provides the eye position information required for visually guided reaching. *Journal of Neurophysiology*, 80(3), 1605–1608.

- Marconi, B., Genovesio, A., Battaglia-Mayer, A., Ferraina, S., Squatrito, S., Molinari, M., et al. (2001). Eye-hand coordination during reaching. I. Anatomical relationships between parietal and frontal cortex. *Cerebral Cortex*, *11*(6), 513–527.
- Mazzoni, P., Bracewell, R. M., Barash, S., & Andersen, R. A. (1996). Motor intention activity in the macaque's lateral intraparietal area. I. Dissociation of motor plan from sensory memory. *Journal of Neurophysiology*, *76*(3), 1439–1456.
- McIntyre, J., Stratta, F., & Lacquaniti, F. (1997). Viewer-centered frame of reference for pointing to memorized targets in three-dimensional space. *Journal of Neurophysiology*, *78*(3), 1601–1618.
- McIntyre, J., Stratta, F., & Lacquaniti, F. (1998). Short-term memory for reaching to visual targets: Psychophysical evidence for body-centered reference frames. *The Journal of Neuroscience*, *18*(20), 8423–8435.
- Medendorp, W. P., Goltz, H. C., Vilis, T., & Crawford, J. D. (2003). Gaze-centered updating of visual space in human parietal cortex. *Journal of Neuroscience*, *23*(15), 6209–6214.
- Mountcastle, V. B., Lynch, J. C., Georgopoulos, A., Sakata, H., & Acuna, C. (1975). Posterior parietal association cortex of the monkey: Command functions for operations within extrapersonal space. *Journal of Neurophysiology*, *38*(4), 871–908.
- Musallam, S., Corneil, B. D., Greger, B., Scherberger, H., & Andersen, R. A. (2004). Cognitive control signals for neural prosthetics. *Science*, *305*(5681), 258–262.
- Mushiake, H., Tanasugu, Y., & Tanji, J. (1997). Neuronal activity in the ventral part of premotor cortex during target-reach movement is modulated by direction of gaze. *Journal of Neurophysiology*, *78*(1), 567–571.
- Nakamura, K., Chung, H. H., Graziano, M. S., & Gross, C. G. (1999). Dynamic representation of eye position in the parieto-occipital sulcus. *Journal of Neurophysiology*, *81*(5), 2374–2385.
- Nanayakkara, T., & Shadmehr, R. (2003). Saccade adaptation in response to altered arm dynamics. *Journal of Neurophysiology*, *90*(6), 4016–4021.
- Pisella, L., Grea, H., Tilikete, C., Vighetto, A., Desmurget, M., Rode, G., et al. (2000). An 'automatic pilot' for the hand in human posterior parietal cortex: Toward reinterpreting optic ataxia. *Nature Neuroscience*, *3*(7), 729–736.
- Pouget, A., Dayan, P., & Zemel, R. S. (2003). Inference and computation with population codes. *Annual Review of Neuroscience*, *26*, 381–410.
- Pouget, A., Ducom, J. C., Torri, J., & Bavelier, D. (2002). Multisensory spatial representations in eye-centered coordinates for reaching. *Cognition*, *83*(1), B1–B11.
- Powell, K. D., & Goldberg, M. E. (2000). Response of neurons in the lateral intraparietal area to a distractor flashed during the delay period of a memory-guided saccade. *Journal of Neurophysiology*, *84*(1), 301–310.
- Robinson, D. L., Goldberg, M. E., & Stanton, G. B. (1978). Parietal association cortex in the primate: Sensory mechanisms and behavioral modulations. *Journal of Neurophysiology*, *41*(4), 910–932.
- Rossetti, Y., & Pisella, L. (2002). Several 'vision for action' systems: A guide to dissociating and integrating dorsal and ventral functions (Tutorial). *Common Mechanisms in Perception and Action*, *19*, 62–119.
- Sabes, P. N., Breznen, B., & Andersen, R. A. (2002). Parietal representation of object-based saccades. *Journal of Neurophysiology*, *88*(4), 1815–1829.
- Salinas, E., & Abbott, L. F. (1995). Transfer of coded information from sensory to motor networks. *The Journal of Neuroscience*, *15*(10), 6461–6474.
- Salinas, E., & Thier, P. (2000). Gain modulation: A major computational principle of the central nervous system. *Neuron*, *27*(1), 15–21.
- Schwartz, A. B., Moran, D. W., & Reina, G. A. (2004). Differential representation of perception and action in the frontal cortex. *Science*, *303*(5656), 380–383.
- Scott, S. H., Sergio, L. E., & Kalaska, J. F. (1997). Reaching movements with similar hand paths but different arm orientations. 2. Activity of individual cells in dorsal premotor cortex and parietal area 5. *Journal of Neurophysiology*, *78*(5), 2413–2426.
- Shadmehr, R., & Wise, S. P. (2005). *The computational neurobiology of reaching and pointing*. Cambridge, Massachusetts: The MIT Press.
- Shen, L. M., & Alexander, G. E. (1997a). Neural correlates of a spatial sensory-to-motor transformation in primary motor cortex. *Journal of Neurophysiology*, *77*(3), 1171–1194.
- Shen, L. M., & Alexander, G. E. (1997b). Preferential representation of instructed target location versus limb trajectory in dorsal premotor area. *Journal of Neurophysiology*, *77*(3), 1195–1212.
- Snyder, L. H., Batista, A. P., & Andersen, R. A. (1997). Coding of intention in the posterior parietal cortex. *Nature*, *386*(6621), 167–170.
- Snyder, L. H., Batista, A. P., & Andersen, R. A. (1998). Change in motor plan, without a change in the spatial locus of attention, modulates activity in posterior parietal cortex. *Journal of Neurophysiology*, *79*(5), 2814–2819.
- Snyder, L. H., Batista, A. P., & Andersen, R. A. (2000). Intention-related activity in the posterior parietal cortex: A review. *Vision Research*, *40*, 1433–1441.
- Snyder, L. H., Grieve, K. L., Brotchie, P., & Andersen, R. A. (1998). Separate body- and world-referenced representations of visual space in parietal cortex. *Nature*, *394*(6696), 887–891.
- Sober, S. J., & Sabes, P. N. (2005). Flexible strategies for sensory integration during motor planning. *Nature Neuroscience*, *8*(4), 490–497.
- Soechting, J. F., Buneo, C. A., Herrmann, U., & Flanders, M. (1995). Moving effortlessly in 3-dimensions—does Donders-law apply to arm movement. *Journal of Neuroscience*, *15*(9), 6271–6280.
- Soechting, J. F., Engel, K. C., & Flanders, M. (2001). The Duncker illusion and eye-hand coordination. *Journal of Neurophysiology*, *85*(2), 843–854.
- Stuphorn, V., Bauswein, E., & Hoffman, K.-P. (2000). Neurons in the primate superior colliculus coding for arm movements in gaze-related coordinates. *Journal of Neurophysiology*, *83*, 1283–1299.
- Torres, E. B., & Zipser, D. (2002). Reaching to grasp with a multi-jointed arm. I. Computational model. *Journal of Neurophysiology*, *88*(5), 2355–2367.
- Vandermeer, A. L. H., Vanderweel, F. R., & Lee, D. N. (1995). The functional-significance of arm movements in neonates. *Science*, *267*(5198), 693–695.
- Vetter, P., Goodbody, S. J., & Wolpert, D. M. (1999). Evidence for an eye-centered spherical representation of the visuomotor map. *Journal of Neurophysiology*, *81*(2), 935–939.
- Wolpert, D. M., Ghahramani, Z., & Jordan, M. I. (1995). Are arm trajectories planned in kinematic or dynamic coordinates? An adaptation study. *Experimental Brain Research*, *103*(3), 460–470.
- Wolpert, D. M., Goodbody, S. J., & Husain, M. (1998). Maintaining internal representations the role of the human superior parietal lobe. *Nature Neuroscience*, *1*(6), 529–533.
- Xing, J., & Andersen, R. A. (2000). Models of the posterior parietal cortex which perform multimodal integration and represent space in several coordinate frames. *Journal of Cognitive Neuroscience*, *12*(4), 601–614.
- Zhang, M., & Barash, S. (2000). Neuronal switching of sensorimotor transformations for antisaccades. *Nature*, *408*(6815), 971–975.
- Zipser, D., & Andersen, R. A. (1988). A back-propagation programmed network that simulates response properties of a subset of posterior parietal neurons. *Nature*, *331*, 679–684.