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

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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.

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

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(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). 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',

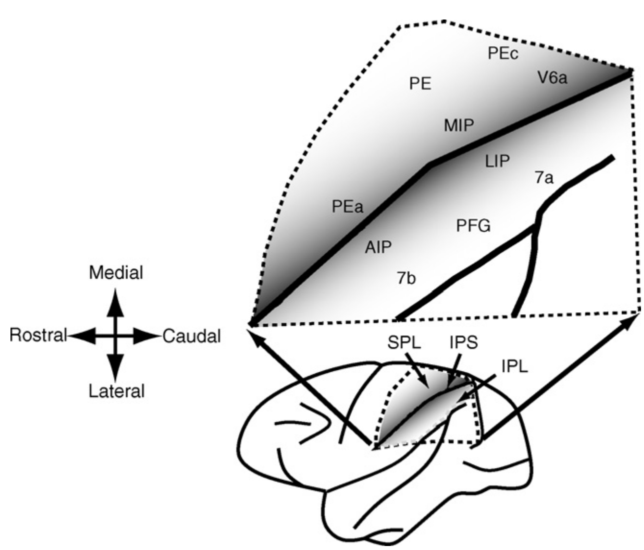

Fig. 1. Lateral view of the macaque monkey brain with the PPC highlighted and expanded. Shaded regions indicate the banks of the intraparietal sulcus (IPS). See text for definitions of abbreviations.

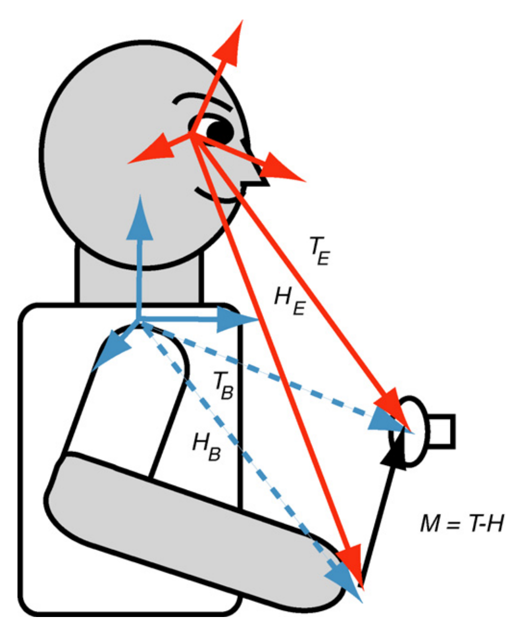

Fig. 2. Schematic showing the reach-related variables described in the text. *T*, target position; *H*, hand position; *M*, motor error; *B*, body-centered coordinates; *E*, eye-centered coordinates.