Visuomotor functions of the posterior parietal cortex

Abstract

In this special issue of Neuropsychologia leading experts in the field discuss controversies and advances in the role of the posterior parietal cortex (PPC) in visuomotor control. The papers are wide-ranging in their scope, covering monkey physiology and anatomy, functional imaging in humans and monkeys as well as transcranial magnetic stimulation and lesion studies in humans. The collection provides an important overview of the current state-of-the-art in this area of research, including discussions on homologies between monkey and human parietal regions, the role of co-ordinate transformations and intermediate representations from vision to action, and reviews of controversial hot topics in this field.

Keywords: Sensorimotor; Reaching; Grasping; Spatial deficits; Optic ataxia; Neglect

This special issue of Neuropsychologia focuses on recent advances in our understanding of the visuomotor functions of the posterior parietal cortex (PPC). Visually guided movements, such as reaching out to grasp an object, ordinarily involve translating visual information that is coded initially in retinotopic coordinates into a motor plan that specifies the sequence of postural changes required to bring the hand to the object. More specifically, information coded in extrinsic (spatial) co-ordinates must be transformed into a motor plan that can be expressed within intrinsic (motor) co-ordinates. The posterior parietal cortex is thought to play a key role in both the representation of corporeal and peripersonal space and in the sensorimotor transformations associated with the planning and control of movement. Consistent with this suggestion, damage to the PPC in humans often leads to disorders in the representation of space (e.g., hemispatial neglect) and to impairments in the planning and control of goal-directed movements (e.g., ideomotor limb apraxia and optic ataxia). While a good deal is already known about the visuomotor functions of the PPC, understanding the nature of the sensorimotor transformations carried out within human PPC remains a fundamental and largely unresolved problem for neuroscience and is potentially of considerable clinical importance in treating the consequences of brain injury and brain disease.

1. Coordinate transformations and the planning and control of visually guided action

A great deal of our current understanding of how sensorimotor transformations are implemented within the PPC comes from electrophysiological recording and lesion studies of non-human primates. These studies have been extremely successful in identifying multiple representations of space in the monkey PPC, each of which is associated with different types or combinations of action (e.g., saccadic eye movements, reaching or grasping movements of the upper limb) (Andersen, Snyder, Bradley, & Xing, 1997). Buneo and Andersen review evidence from recent electrophysiological recording studies that indicate a key role for the primate PPC in context dependent coordinate transformations and in the planning and control of visually guided arm movements. These authors argue persuasively for the important role played by eye-centred representations in the formation of internal ‘forward’ state estimates that may be used to recursively plan and control reaching movements. More specifically,
they suggest that the PPC acts as a sensorimotor interface for visually guided movements within which representations of target position and current hand position in an eye-centered frame of reference can be mapped directly to a representation of motor error in a hand-centered frame of reference. Empirical evidence for the importance of eye-centred coordinates in the planning and execution of visually guided reaching movements is reported in the paper by Dijkerman, McIntosh, Anema, et al. In two experiments these authors studied the pattern of reaching errors made by two patients presenting with non-foveal optic ataxia following right hemisphere PPC damage. By varying the location of fixation and the orientation of the head and body these authors were able to establish that reaching errors made to visual targets were consistently to the left of the current direction of gaze, rather than to the left of head-, body-, or limb-relative space.

The role played by the PPC in producing context dependent coordinate transformations is also addressed within the paper by Battaglia-Mayer, Archambault and Caminiti. Whereas Buneo and Andersen argue for the primacy of an eye-centred reference frame within which reaching movements are planned and controlled, Battaglia-Mayer et al. propose a more dynamic and context-dependent scheme and emphasise how PPC neurons are ideally suited to facilitate eye-hand coordination during reaching. Their paper describes how neurons in the superior (SPL) and inferior (IPL) parietal lobules are modulated by a variety of signals associated with planning and execution of eye and hand movement, and how there is often an invariance in the directional tuning properties of PPC neurons across tasks that require different forms of spatial relationship between the eye and the hand. They propose that the impaired reaching movements observed in patients with optic ataxia might be interpreted as a consequence of the breakdown of the combinatorial mechanisms of parietal neurons. This proposal forms a recurring theme in several of the papers within this special issue (see papers by Coulthard et al., Himmelbach et al., Pellijeff et al., and Pisella et al., this issue).

Although there is considerable evidence in support of the view that eye-centred coding is important to the planning and control of reaching movements in many circumstances—particularly for reaching movements directed toward visual objects that located in central vision (see papers by Dijkerman et al., Himmelbach et al., Pisella et al., this issue)—an attractive aspect of the combinatorial network scheme is that it allows for different frames-of-reference to be dynamically created according to task context. One situation where an eye-centred frame-of-reference may be less than optimal might be when reaching to non-foveated target objects (i.e., visual objects that are located in peripheral vision), as it has been argued that in these circumstances it may be important to de-couple the direction of a reaching movement from gaze direction (Jackson, Newport, Mort, & Husain, 2005).

2. Functional homologies between monkey and human posterior parietal cortex

Electrophysiological recording studies of non-human primates have been extremely successful in identifying multiple representations of space in the monkey PPC, each of which is associated with different types or combinations of action. However, despite the success of these studies their relevance to understanding how the human PPC represents space and contributes to the planning and control of goal-directed movements remains to be clearly demonstrated and can be questioned on a number of grounds.

An alternative approach to single-unit recording studies of monkey PPC is to study human parietal function directly using functional neuroimaging techniques. The paper by Culham, Pratesi and Singhal discusses the technical challenges involved in studying realistic movements in a brain imaging environment, and reviews recent human neuroimaging studies of visuomotor function. Culham et al. report that neuroimaging studies have already identified putative functional equivalents of the following macaque regions: parietal eye fields (PEF), ventral intraparietal (VIP) area, the sub-regions that make up the so-called parietal reach region (PRR) and the anterior intraparietal (AIP) area. This paper therefore confirms that while there is a growing number of studies that have made use of functional brain imaging techniques (e.g., fMRI) to investigate brain activity associated with visuomotor control mechanisms in humans, these studies can thus far be characterised largely as attempts to identify human homologues of functional brain regions identified previously within the monkey PPC rather investigations that seriously entertain the question that the functional organisation of monkey and human PPC may differ.

While there is considerable enthusiasm for the integration of the results from human brain imaging studies with monkey single-unit recording studies, establishing functional homologies between the monkey and human PPC is not straightforward. One of the major difficulties in drawing anatomical and functional correspondences between monkey and human PPC is that the parietal cortex is considerably expanded in humans compared to the macaque brain. The implications of this expansion are considered within several of the papers appearing within this special issue. Marco Iacoboni argues in his paper that the idea that the largest difference between the human and monkey brain occurs within the parietal lobe should be considered a ‘meme’ (a culturally transmitted idea) that originated following the work of Brodmann. Iacoboni proposes that the Brodmann model of parietal anatomy is incorrect and that the parietal lobe of macaques and humans show similarities and differences comparable to other parts of the brain. He argues that recent functional imaging studies support the concept of good continuity and physiological similarities between macaque and human posterior parietal areas concerned with visuomotor integration. A contrasting perspective on this issue is offered within the paper by Orban et al. who suggest that the expansion of PPC in the human brain may have given rise to regions that are evolutionarily new and provide functional capacities that are not apparent in the monkey PPC.

Many of the theoretical and technical obstacles to comparing human brain imaging and monkey single-unit recording studies are reviewed in the paper by Orban, Claeys, Nelissen et al., who argue that most of the difficulties involved in establishing homologies between areas identified in the monkey using electrophysiological recording techniques and regions identified...
in man using fMRI can be overcome if the same brain imaging technique is used in humans and monkeys (e.g., fMRI). In their paper they review fMRI studies that were conducted in parallel in humans and awake monkeys and which report activations located in the vicinity of the intraparietal sulcus (IPS). They report that the fMRI response to a range of visual stimuli indicate that the human IPS contains more functional regions along its anterior–posterior extent than are known in the monkey. Specifically, whereas the monkey IPS contains only one motion sensitive area (area VIP), which is not particularly sensitive to three-dimensional structure from motion (3D SFM), the human IPS includes four motion sensitive regions which are all sensitive to 3D SFM. The human and monkey IPS also differ in their representation of central vision and it is suggested that the additional cortical tissue in human PPC may provide the capacity for an enhanced visual analysis of moving images necessary for sophisticated control of manipulation and tool handling.

Transcranial magnetic stimulation (TMS) offers an alternative neuroimaging technique to that provided by fMRI. TMS and fMRI complement each other well and both have been used to investigate the contribution of the PPC to visuomotor control. However, TMS offers two advantages over fMRI. First, it offers excellent temporal resolution. Second, it provides for the transient disruption of ongoing brain activity thereby creating relatively localized ‘virtual lesions’. This allows causal relationships to be drawn between brain anatomy and behaviour. The papers by Iacoboni and by Rushworth and Taylor each review TMS studies of PPC function linked to visuomotor control.

The central premise addressed within the Iacoboni paper is that visuomotor control in the PPC is implemented by coding action goals. Iacoboni reviews evidence for the lateralisation of visuomotor functions in the posterior parietal cortex and poses that the left posterior parietal cortex is more concerned with tool use while the right posterior parietal cortex is associated with the imitation of the actions of others.

Rushworth and Taylor present a wide-ranging review of the effects that TMS has on the execution of a variety of visuomotor behaviours, including both attention and intention tasks. A theme that emerges from this review is that TMS disrupts performance when eye or limb movements are executed, or, in circumstances in which attentional/intentional processes that precede such overt movements are required (e.g., the updating of sensorimotor representations prior to movement execution).

3. Updating representations of corporeal and peripersonal space in the PPC

It is thought that the PPC participates in actively maintaining a continuously updated representation of the current configuration of the body and its parts that is specified in intrinsic (postural) coordinates. This representation conforms to the notion of a body schema as proposed by Head and Holmes (1911). Moreover, when we make use of a hand-held tool it becomes an extension of our hand, both physically and perceptually and becomes incorporated within our body-schema. Physiological evidence in support of this proposal has been provided by the elegant and influential studies of Atsushi Iriki and his colleagues who investigated the role played by the PPC in the manipulation of hand held tools. This group demonstrated that bimodal neurons recorded from within monkey intraparietal sulcus dynamically altered their visual receptive field properties following a period of training with a hand held tool (Iriki, Tanaka, & Iwamura, 1996). More specifically they showed that prior to tool use training the visual receptive fields of IPS neurons included only the space around the monkey’s hand. However, after tool-use training the visual receptive fields of these same neurons had expanded to include the space at the tip of the tool.

In the current issue Hihara, Notoya, Tanaka et al. report an investigation into the nature of the neuronal changes in PPC that accompany training with a hand held tool. These authors report that prior to training with a hand held tool the majority of neurons recorded from the IPS of naive monkeys respond uni-modally to somatosensory stimuli. However, after training these same neurons respond bimodally to somatosensory and visual stimulation. To investigate the basis for this change in response, Hirara et al. compared the projection patterns between visually related areas and the intraparietal cortex in trained and naive monkeys using tracer techniques. They report the emergence of novel projections to the IPS from the temporoparietal junction and ventrolateral prefrontal cortex in monkeys trained in tool-use, but not in naive monkeys. This exciting new finding provides evidence for the induction of novel neural connections in the adult monkey PPC that accompanies tool use training.

The role played by multimodal neurons in the monkey PPC in representation of corporeal and peripersonal space is also considered in the paper by Michael Graziano and Dylan Cooke. These investigators describe how two interconnected regions in the frontal (area PZ, precentral gyrus) and parietal (area VIP, intraparietal sulcus) are activated to visual, tactile, and auditory stimuli, respond to objects touching or looming toward the body surface, and produce complex defensive-like withdrawing or blocking movements when stimulated electrically. Graziano and Cooke suggest that these areas may implement a neuronal network that functions to construct a representation of the safety margins around the body and participates in the selection and coordination of defensive behaviour.

As noted in the paper by Buneo and Andersen, while motor errors can be defined as a difference in extrinsic or endpoint space, or as a difference in intrinsic ‘postural’ space (i.e., joint angles or muscle lengths), it is frequently assumed that motor errors are defined within the PPC in extrinsic space (e.g., the eye-centred coordinates associated with the parietal reach region [PRR]). The role played by the human PPC in maintaining and updating postural (i.e., non-visual) representations of the upper limb that participate in the accurate control of reaching movements was investigated using event-related fMRI in the paper by Pelljjeff, Bonilha, Morgan et al. These investigators studied reaching movements executed within the MR scanner without vision from variable, posturally defined, start locations. A key aspect of this study was the comparison of reaches made from novel or repeated start positions. The authors report that a change in the posture of the upper-limb is associated with a significant
increase in BOLD activation in only one brain region—the medial aspect of superior parietal cortex (precuneus). It is interesting to note that this brain area corresponds to a region of PPC previously identified as the human homologue of the monkey PRR.

4. Reaching movements directed to objects in central or peripheral vision

The electrophysiological studies reviewed by Buneo and Andersen confirm the importance of eye-centred coding in the planning and control of visually guided reaching movements. Converging evidence for this view also comes from studying the pattern of movement errors made by optic ataxia (OA) patients when reaching toward visually defined objects (see paper by Dijkerman et al.). Although OA has most often been considered to be a general disorder of visual guided movements, it has long been recognised that the majority of OA patients only exhibit spatial errors when reaching to objects presented in their peripheral visual field. This distinction, between representations of central and peripheral visual fields, is the focus of several of the papers appearing in this special issue.

The paper by Pisella, Binkofski, Lasek et al. considers a wide range of topics related to the disorder of OA. One noteworthy issue raised by these authors is that many of the assumptions that underlie popular models of visuomotor function based upon neuropsychological double-dissociations have rarely been tested experimentally, and lack empirical support. They cite the double-dissociation between visual form agnosia and optic ataxia (frequently cited as support for the popular two visual systems distinction between perception and action) as a case in point.

Pisella et al. also consider evidence that OA may reflect a functional dissociation between central and peripheral vision, and distinguish between ‘field’ and ‘hand’ effects in this context (Perenin & Vighetto, 1988). They suggest that (a) recent unpublished evidence by their group confirms that ‘field’ and ‘hand’ errors are additive and therefore suggestive of dissociable processes, (b) reaching errors associated with ‘field’ effects are linked to eye-centred representations of visual targets within the PPC, and (c) errors associated with ‘hand’ effects result from a mislocalisation of the contralesional (ataxic) limb arising due to an impairment in the processing of proprioceptive information. A similar proposal is made in the paper by Pelljijeff et al. who also associate ‘field’ effects with impaired eye-centred coordinates and ‘hand’ effects with disordered postural representations but link these effects to functional differences between right and left hemisphere PPC respectively.

Additional evidence for a functional dissociation between central and peripheral vision that is linked to OA is provided in the papers by Himmelbach, Karnath, Perenin, et al. and by Newport and Jackson (this volume). Himmelbach, Karnath, Perenin, et al. investigated the hypothesis that OA patients exhibit a general impairment in the ability to carry out fast corrective movements such as in the case of a visual target that changes its spatial location during a reaching movement. They reasoned that in such circumstances the ability to carry out on-line correction is also confounded by the target jumping into the peripheral visual field. To dissociate these two effects Himmelbach et al. introduced a perturbation that required on-line correction – a change in object size – but where the target remained throughout within central vision. The authors tested the same patient (I.G.) who was reported previously to be impaired in executing on-line corrections during reaching movements (Pisella, Grea, Tiliakete, Vighetto, Desmurget, & Rode, 2000) and demonstrated that her ability to adjust her grip aperture on-line was similar to healthy control subjects.

The paper by Newport and Jackson investigates adaptation to optical prisms in a patient (J.J.) with non-foveal OA. Prism adaptation offers an interesting behavioural probe of PPC function for at least two reasons. First, the PPC is thought to contribute to the ‘strategic’ component of prism adaptation that has been linked with mechanisms involved in the rapid, on-line, correction of movement errors (see above). Second, successful adaptation to optical prisms necessitates that an individual learns to dissociate gaze direction from the direction of their reaching movement. It is suggested that reaching movements directed to targets away from fixation (i.e., in peripheral vision) may depend to a large extent upon postural coding mechanisms (Jackson et al., 2005). The data from patient J.J. indicate that the ability to implement control strategies may not be necessary for successful adaptation to prisms.

A recent functional neuroimaging study has confirmed that reaching movements directed to foveal and extrarfoveal visual target locations activate quite different regions of PPC (Prado et al., 2005). Reaching movements to targets presented in peripheral vision activates a region within the parieto-occipital-junction (POJ), whereas reaching to targets presented in central or peripheral vision activates a region of the medial intraparietal sulcus (mIPS). It is interesting to note in this context that the mIPS region observed by Prado et al. (2005) corresponds to the region of the human PPC that is: expanded relative to the monkey PPC; sensitive to three-dimensional structure from motion; and has been linked to an increased use of tools in humans (Orban et al., this volume).

The anatomical correlates for different patterns of visuomotor deficit following unilateral brain damage are addressed in the paper by Coulthard, Parton and Husain (this volume). These authors review the pattern of reaching impairments observed in neurological patients presenting with unilateral neglect, optic ataxia, or both. When considering unilateral neglect Coulthard et al. discuss the directional and spatial deficits that may contribute to reaching abnormalities, and highlight the importance of target selection and on-line guidance. They also examine the relationship between optic ataxia and neglect by considering two illustrative cases, one with pure optic ataxia and the other with optic ataxia plus neglect that reveal some important issues regarding the (controversial) anatomical bases of these syndromes.

Some of the students we teach – and even occasionally some of our colleagues – have the impression that the interesting issues about the parietal cortex have been dealt with quite a long time ago. Readers of this Special Issue will see very clearly that this is far from being the case. We have really enjoyed editing the papers in this collection. They have been stimulating
and provocative, often questioning current dogma in a way that is unfortunately not usually possible in standard journal submissions. We hope that you will be engaged by some of these contributions as much as we have, and that these papers serve as a catalyst to stimulate debate on parietal contributions to visuo-motor control.

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