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Visuo-motor integration and control in the human posterior parietal cortex: Evidence from TMS and fMRI

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Abstract

The posterior parietal cortex is a fundamental structure for visuo-motor integration and control. Here I discuss recent transcranial magnetic stimulation (TMS) and functional magnetic resonance imaging (fMRI) studies that I interpret as suggesting four concepts. The evolutionary process has enlarged the human posterior parietal cortex while still preserving the internal structure of the posterior parietal cortex of other primates. Visuo-motor control in the posterior parietal cortex may be implemented by coding primarily action goals. The lateralization of visuo-motor functions in the posterior parietal cortex suggests that the left posterior parietal cortex is more concerned with tool use and the right posterior parietal cortex is more concerned with imitation of the actions of others. Finally, visuo-motor inter-hemispheric transfer through parietal callosal fibers occurs at the level of 'motor intention'.

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In anatomical terms, the parietal lobe is strategically located between vision (occipital lobe) and action (frontal lobe). This anatomical localization makes the parietal lobe, especially in its posterior sectors (i.e., posterior to the postcentral sulcus), an ideal structure for visuo-motor integration. In this special issue of *Neuropsychologia*, we are all trying to tackle different aspects of visuo-motor integration supported by parietal structures. To do so, we discuss a variety of investigative approaches. In this paper, I would like to discuss findings from transcranial magnetic stimulation (TMS) and functional magnetic resonance imaging (fMRI) studies in humans that are particularly relevant to two aspects of visuo-motor functions in the posterior parietal cortex: the coding of action goals in visuo-motor control, and the lateralization of visuo-motor functions and their integration through callosal fibers. Obviously, these are only two of the many aspects of parietal functions that are currently investigated. The conclusions that one can reach with regard to basic principles of parietal organization while discussing these issues may not be generalized to other functions.

Although the studies I discuss have mainly involved human participants, the interpretation of their findings rely strongly on animal data, in particular anatomical and single-unit data in monkeys. Thus, I believe it is necessary to explicitly address up front the relationships between the two species and between the techniques adopted in the two species. First of all, what are the anatomical homologies between monkey and human posterior parietal cortex? Second – given that the majority of physiological data available in monkeys and humans are derived, respectively, from single-unit investigations and fMRI experiments – what are the relationships between single-unit data and the fMRI signal?

1. Anatomical maps of the primate parietal cortex

I have a strong interest in imitation and all sorts of mimetic processes. Recently, in the study of culture, there has been an active borrowing of concepts deriving from evolution and biology (Aunger, 2000). One of the most successful of these concepts is the concept of 'meme', a cultural unit transmitted by non-genetic means (Dawkins, 1976). I think that a powerful meme in neuroscience is the one propagated by the cytoarchitectonic maps of Brodmann, suggesting that the largest differences between monkey and human brain are observed in the parietal

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lobe. This idea stems from Brodmann maps showing area 5 in the superior parietal lobule and area 7 in the inferior parietal lobule in macaques, whereas in humans both area 5 and 7 are located in the superior parietal lobule, while the inferior parietal lobule contains the human specific areas 40 and 39, products of a supposedly quite fast evolutionary cortical process (Zilles & Palomero-Gallagher, 2001).

This idea seems also supported by the fact that parietal lesions in humans and monkeys have different consequences. However, this is hardly surprising, considering that human lesions are naturally occurring ones, whereas animal lesions are experimental ones. Moreover, humans and monkeys have obviously different cognitive capacities. To have a sense of the similarities and differences in human and monkey posterior parietal cortex, I believe it is important to start from anatomical facts.

Brodmann's map became the most dominant anatomical model in systems neuroscience, thus practically obscuring the work of several other anatomists that all converge in supporting stronger homologies between human and monkey posterior parietal cortex. This work suggests that the differences between human and monkey posterior parietal regions are similar to those observed in other parts of the brain. For instance, the work of von Bonin and Bailey in the macaque brain (von Bonin & Bailey, 1947) and of von Economo in the human brain (von Economo, 1929) suggests similarities between the superior and inferior parietal lobules in the two species, with the superior parietal lobule corresponding to area PE and the inferior parietal lobule corresponding to area PF rostrally and PG caudally. Moreover, the maps of von Economo suggest a subdivision of these areas in several sub-areas, a concept supported – and even expanded – by the Vogt school (Zilles & Palomero-Gallagher, 2001) and more recently by quantitative receptor distribution studies (Scheperjans, Grefkes, Palomero-Gallagher, Schleicher, & Zilles, 2005; Zilles et al., 2002; Zilles, Palomero-Gallagher, & Schleicher, 2004). Anatomical models with heterogeneous subareas also fit much better the high degree of areal differentiation that emerges from single-unit and functional imaging studies (Rizzolatti & Matelli, 2003; Zilles et al., 2004). For all these considerations, it is very likely 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. Several recent functional imaging studies support the concept of continuity and physiological similarities between macaque and human posterior parietal areas concerned with visuo-motor integration. However, these studies – that I will discuss later on – beg the question: how does one go from single-unit recordings in macaques to fMRI in humans?

2. Single-unit and BOLD signal

The work of Logothetis and colleagues, measuring spike density function, multi-unit activity and local field potential while also measuring blood oxygenation level dependent (BOLD) fMRI signal in macaque visual areas during visual stimulation, is highly relevant here (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001). What the empirical data show is that there is – as frankly expected – a relatively nice anatomical co-localization of neural and BOLD signal in visual cortex. The degree of co-localization between neural and BOLD signal really depends on the level of spatial resolution one wants to investigate. At the level of resolution of the majority of fMRI studies published in peer-reviewed journals (and practically all the studies reviewed here with regard to visuomotor control in the posterior parietal cortex), the simultaneous neural and BOLD recordings show a substantially perfect co-localization (Logothetis, 2003; Logothetis & Wandell, 2004). However, studies on neurovascular coupling using simultaneous optical imaging and neural recordings have demonstrated that the delayed hemodynamic response does not co-localize precisely with the changes in neuronal activity (Malonek & Grinvald, 1996; Thompson, Peterson, & Freeman, 2003). What really co-localizes well with neural activity in 'vascular' terms is the initial increase in deoxyhemoglobin concentration that corresponds in BOLD signal to the so-called 'initial dip' (Buxton, 2001; Yacoub et al., 2001), a phenomenon that can be imaged reliably only at high fields and that is too small in magnitude to be tractable with current statistical approaches in functional neuroimaging.

With regard to the temporal correlation between neural and BOLD signal, BOLD – as expected – lags quite behind the neural response (Logothetis, 2003; Logothetis et al., 2001; Logothetis & Wandell, 2004). However, beyond this delayed response, the really important question for people interpreting human fMRI data in light of neural recordings in non-human primates is whether there is a good relationship between the time-course of the BOLD signal and the time-course of neural activity. Using linear-time invariance methods that assume linearity-dependent BOLD response to neural signal – an assumption not entirely true but still quite accurate as first approximation – Logothetis and colleagues have shown that neural estimates of BOLD time course are relatively accurate for short stimulus presentations, but become less accurate for longer stimulus presentations (Logothetis et al., 2001; Logothetis & Wandell, 2004). This is particularly true for spikes and multi-unit activity – neural parameters that are supposed to be more relevant to the output of a given brain region – whereas the local field potential – a neural parameter that is supposed to be more relevant to the input of a brain region – seems to correlate well with BOLD even at longer stimulus presentations. Overall, the local field potential performed reliably better than multi-unit in predicting the BOLD signal (Logothetis et al., 2001; Logothetis & Wandell, 2004). Hence, the proposal that BOLD fMRI reflects more the input rather than the output of a brain area.

Under normal circumstances, however, input and output in a brain area should also correlate, at least in the cerebral cortex, maybe less so in the cerebellum (Mathiesen, Caesar, Akgoren, & Lauritzen, 1998; Mathiesen, C., Caesar, & Lauritzen, 2000), thus making a strong correlation between action potentials and BOLD quite plausible. In fact, when human BOLD data from MT/V5 were compared to spiking activity from single-unit recordings in macaque MT/V5, a strong correlation was observed, with a proportionality constant of approximately nine action potentials per second per unit and per percentage of BOLD increase (Rees, Friston, & Koch, 2000).

A more direct demonstration of the strong link between action potentials and BOLD has been recently provided in humans. Single units in human auditory cortex were recorded with intracranial depth electrodes implanted for potential surgical treatment. The patients were shown a segment of a movie, ‘The good, the bad, and the ugly’ by Sergio Leone. The spiking activity in these neurons was converted into a predicted BOLD time-series by convolving it with a Gamma function, a typical hemodynamic response function used in imaging processing. The predicted BOLD time-series was then used as a regressor for fMRI data obtained in healthy subjects while they watched the same segment of the movie. BOLD signal in auditory cortex in healthy volunteers was strongly correlated with the action potentials recorded with depth electrodes in epileptic patients (Mukamel, Gelbard, Arieli, Hasson, Fried, & Malach, 2005).

Taken together, these data suggest that it is safe to make comparisons between BOLD fMRI findings and single-unit recordings. The next section of the paper indeed discusses fMRI results that in light of single-unit data in macaques—suggest strong functional homologies between the human and the monkey posterior parietal cortex.

3. Functional homologies between monkey and human posterior parietal cortex

In the previous sections, we have seen that anatomical data suggest similarities between monkey and human posterior parietal cortex. Moreover, data on neural recordings and BOLD fMRI in monkeys and humans also suggest a good relationships between spikes and BOLD. Given that these two foundational conditions are satisfied, we can now look into the functional homologies between monkey and human posterior parietal cortex in a variety of experiments investigating visuo-motor transformations. Neurophysiological studies in non-human primates have identified several posterior parietal areas with specific neurophysiological properties.

Rostrally, the anterior intraparietal area (AIP), is concerned with grasping objects and with the analysis of object properties, such as size, shape, orientation (Murata, Gallese, Kaseda, & Sakata, 1996; Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Sakata, Taira, Murata, & Mine, 1995; Taira, Mine, Georgopoulos, Murata, & Sakata, 1990). Similarly, a variety of functional neuroimaging studies have reported increased activity in an anterior sector of the human intraparietal sulcus during grasping and during perceptual tasks requiring object analysis (Binkofski et al., 1999a,b; Chao & Martin, 2000; Frey, Vinton, Norlund, & Grafton, 2005; Grefkes, Weiss, Zilles, & Fink, 2002).

Still quite anteriorly, but more in the depth of the intraparietal sulcus, neurophysiological studies in macaques have described an area, called the ventral intraparietal area (VIP), that is relevant to the processing of polymodal moving stimuli. Neurons in VIP respond to visual, tactile, and auditory stimuli (Colby, Duhamel, & Goldberg, 1993; Duhamel, Colby, & Goldberg, 1998; Schlack, Sterbing-D’Angelo, Hartung, Hoffmann, & Bremmer, 2005). Area VIP in the posterior parietal cortex is strongly connected with area F4 in the ventral premotor cortex of macaques (Rizzolatti & Luppino, 2001). Neurons in F4 have neurophysiological properties similar to VIP neurons (Graziano & Gross, 1998). The VIP-F4 circuit in macaques is thought to be important for creating a peripersonal space map (Rizzolatti & Matelli, 2003) and for controlling defensive movements (Cooke, Taylor, Moore, & Graziano, 2003; Graziano, Taylor, Moore, & Cooke, 2002). Similarly, functional neuroimaging data in humans show that tactile, visual, and auditory moving stimuli all activate an area in the depth of the human intraparietal sulcus, the human homologue of macaque VIP, and even a premotor area that is likely the human homologue of macaque F4 (Bremmer et al., 2001).

More posteriorly, the intraparietal cortex of the macaque contains areas concerned with the planning of eye movements (lateral intraparietal area, LIP) (Colby, Duhamel, & Goldberg, 1996), and with the planning of arm and hand reaching movements (medial intraparietal area, MIP) (Snyder, Batista, & Andersen, 1997). Area LIP is located on the lateral bank of the sulcus, whereas area MIP is located more posteriorly, and on the medial bank of the sulcus. A similar topographic pattern of two human intraparietal areas concerned with eye movement planning and hand movement planning was observed in a recent fMRI study on task switching (Rushworth, Paus, & Sipila, 2001c). The visual task switching activated preferentially an area in the lateral bank of the sulcus (putative human LIP), whereas the response hand task switching activated preferentially an area in the medial bank of the intraparietal sulcus (putative human MIP). A subsequent imaging study from a separate group (Astafiev et al., 2003), confirmed a similar relative positioning of putative human LIP and MIP. This study, however, also mapped the functional activation onto a macaque brain by using surface-based registration approaches. This procedure suggested that – even though the relative positioning of putative human LIP and MIP may be similar to the relative positioning of the macaque LIP and MIP – in the human both LIP and MIP may be located in the medial bank of the intraparietal sulcus.

Neuronal properties similar to area MIP in macaques are also observed in the adjacent superior parietal lobule (SPL) (Battaglia-Mayer et al., 2000; Caminiti, Ferraina, & Johnson, 1996; Ferraina et al., 2001). Taken together, these areas form what is called the macaque parietal reach region (PRR). In humans, fMRI studies have disclosed that an anatomically similar parietal region is endowed with functional properties also similar to PRR neurons (Connolly, Andersen, & Goodale, 2003; Grefkes, Ritzl, Zilles, & Fink, 2004).

Human brain imaging studies on grasping (Culham et al., 2003; Grafton, Fagg, Woods, & Arbib, 1996), however, have shown that posterior sectors of human SPL are activated not only during reaching but also during grasping. In macaques, until recently, the evidence suggested that the posterior part of SPL had only neurons responding to reaching but not grasping, suggesting a functional difference in this sector of the posterior parietal cortex between monkeys and humans. Recently, however, single-unit evidence of neuronal activity modulation during the last phase of prehension were reported in area V6A, a visuomotor area located in the caudal part of the posterior parietal cortex (Fattori, Breveglieri, Amoroso, & Galletti, 2004). This evidence supports homologies between monkeys and humans not only in the anterior sectors of the posterior parietal cortex, but also in its posterior sector.

Taken together, all these findings support a model that accounts for the preferential expansion of the human posterior parietal cortex compared to the posterior parietal cortex in monkeys by assuming that the relative enlargement in humans had preserved a similar architectural plan between the two species (Astafiev et al., 2003; Van Essen et al., 2001).

4. Planning and control of action: role of posterior parietal cortex

The posterior parietal cortex is a critical structure for the planning and control of actions (Jeannerod, 1997; Milner & Goodale, 1995). In the last few years, TMS and functional neuroimaging have been used to investigate in details the relationships between the posterior parietal cortex and visuo-motor control. TMS and functional neuroimaging are two techniques that complement each other very well in the study of brain–behavior relationships. Functional neuroimaging, especially fMRI, achieves a satisfactory spatial resolution that gives detailed anatomical information on brain areas relevant to different forms of behavior. The type of information that functional neuroimaging can provide, however, is only correlative. No causal relationships between the activity in a given brain area and the behavior under investigation can be achieved with functional neuroimaging. TMS, on the other hand, by directly interfering with ongoing neural activity to create transient 'virtual lesions', provides exactly the information on causal relations between brain and behavior that cannot be provided by imaging techniques. Moreover, TMS has an exquisite temporal resolution, allowing a detailed investigation of visuo-motor control while it unfolds over time. In this section of the paper, I would like to discuss recent advances in our understanding of the role of the posterior parietal cortex in visuo-motor planning and control provided by TMS and functional neuroimaging studies.

The dichotomy between planning and control in visuo-motor behavior is an old one (Woodworth, 1899), and has generated, and still generates, much debate (Glover, 2004). In terms of brain structures, the posterior parietal cortex has been strongly implicated in both planning and control. Recent TMS studies have revived much interest in the role of posterior parietal areas in feed-forward planning and feedback control. For instance, a group of subjects were asked to 'look and point' with the right hand to peripheral visual targets. In some trials, the target jumped. Subjects were able to correctly point to both stationary and jumping targets, a finding consistent with previous reports (Milner & Goodale, 1995). When single TMS pulses were applied over the left posterior parietal cortex, subjects were still able to correctly reach the stationary target, but were unable to correct the aiming trajectory in the jumping target trials (Desmurget et al., 1999). These results suggest that the movement was planned before its onset and that the posterior parietal cortex seems responsible for updating the motor plan on the basis of visual feedback. But what kind of 'visual' feedback was disrupted by the TMS pulse? When subjects were asked to use their left hand and were stimulated on the left posterior parietal cortex, no effect of TMS was observed. This suggests that TMS did not really perturb target localization and that its effect is more 'motor' than 'visual'. Possible TMS effects may have interfered with the estimation of the hand position, with the computation of the motor error, and with the corrective signal.

The same group published recently another TMS study over the posterior parietal cortex with the intent of perturbing on line adjustment of grasping actions (Tunik, Frey, & Grafton, 2005). Classically, reaching and grasping are conceived as separate, dissociable processes (the so-called 'visuo-motor channel hypothesis') (Jeannerod, 1988, 1997). The neural correlates of reaching would be SPL and dorsal premotor cortex, whereas the neural correlates of grasping would be the anterior inferior parietal and intraparietal cortex, and the ventral premotor cortex (Jeannerod, 1997). If one looks at the results of the two studies, they seem to show a nice dissociation between grasping and reaching, in terms of TMS effects. Indeed, in the more recent study (Tunik et al., 2005), subjects are asked to grasp an object. In some trials, the orientation of the object is perturbed. Interestingly, two experiments were performed. In one experiment, subjects were instructed to adjust by changing only their grip aperture, and by always keeping their index finger and thumb oriented along a vertical axis. In the second experiment, subjects were told they had to grasp only the narrow dimension of the object. Hence, they made online adjustments by rotating their wrist, and not by changing their grip aperture. TMS applied over the posterior parietal cortex produced an effect only in perturbed trials in both experiments. This suggests that, as in the previous reaching and pointing experiment (Desmurget et al., 1999), the motor plan was fully developed at the onset of the movement. The fact that online adjustments of both grip aperture (Experiment 1) and wrist orientation (Experiment 2) were disrupted by TMS during perturbed trials even though the same posterior parietal site was stimulated, argues against a strong somatotopic organization of parietal regions, at least for online adjustments. In fact, changes in grip aperture and wrist orientation involve different motor effectors, fingers in the first case, wrist in the second one. Moreover, TMS effects were observed only for early stimulation (65 ms) with respect to the object perturbation. Late stimulations did not produce the effect, suggesting that the TMS effect had to do with the initiation of the online correction. Finally, in both experiments of the more recent study (Tunik et al., 2005), the reaching component seemed unaltered by TMS.

At first sight, these two TMS studies over the posterior parietal cortex seem to support the visuo-motor channel hypothesis. One study shows an effect on online adjustments of reaching (Desmurget et al., 1999), and the other one shows an effect on online adjustment of grasping but not reaching (Tunik et al., 2005). However, if one looks at the stimulation sites in both studies (Fig. 1), it seems that the same posterior parietal region is stimulated, even though in one case (Desmurget et al., 1999) reaching is disrupted, and in the other case (Tunik et al., 2005), grasping adjusting grip aperture, and grasping adjusting wrist orientation, are disrupted. In all cases, the only unifying factor is that what is disrupted is the goal of the action, what the

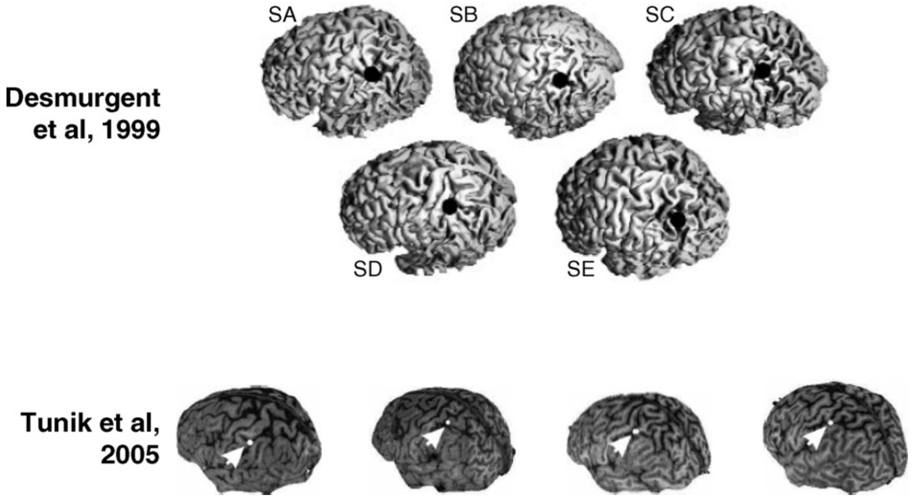

Fig. 1. Stimulation sites of two TMS studies showing disruption of online adjustments of reaching movements (Desmurget et al., 1999) and of grasping movements (Tunik et al., 2005). The sites of stimulation are practically indistinguishable, being located in both studies in the anterior part of the intraparietal cortex. Modified from original figures of the two articles with permission.

subject was supposed to achieve, i.e., reach the target, or grasp the object. Thus, the real novelty of the data provided by these TMS studies is that – no matter what is the motor effector (finger, wrist) and no matter what is the task (reaching, grasping) – the anterior sector of the intraparietal cortex (see Fig. 1) is concerned with online adjustments that are necessary to achieve the goal of the visuo-motor task.

Two more recent TMS studies over the posterior parietal are also important here. In these two studies, the stimulation sites were more posterior and more medial than the stimulation sites of Desmurget et al. (1999) and of Tunik et al. (2005). The standard space coordinates provided by the two studies suggest a very similar site of stimulation (approximately $x = 30$, $y = -60$, $z = 60$), considering the spatial resolution of TMS (Walsh & Cowey, 2000). One of these two studies focused on online adjustments of grasp perturbation (Glover, Miall, & Rushworth, 2005), whereas the other one was concerned with the adaptation of arm trajectory in a velocity-dependent force-field (Della-Maggiore, Malfait, Ostry, & Paus, 2004). Both studies demonstrated that the posterior parietal cortex is essential to the adjustment of motor commands. Both studies also concurred in supporting the idea that – in order to interfere with the motor adjustments – TMS pulses must be delivered around the initiation of the motor adjustment. In fact, one study clearly shows that if the timing of the TMS pulse misses this specific time window, no effect is observed.

How to interpret these results? In the four TMS studies I discussed above, two major sectors of the posterior parietal cortex were stimulated, the anterior and mid-IPS. Both stimulation sites were associated with disruption of adjustments of two different motor effectors, finger and wrist in the anterior sector, and finger and arm in the more medial and posterior sector. These non-specific effects in terms of the motor effector involved may simply represent lack of spatial resolution of the TMS technique. However, single-pulse TMS is successfully used for motor mapping at spatial resolutions lower than what appears to be the distance between these posterior parietal stimulation sites. Thus, it is unlikely that the lack of motor effector specificity is due to spatial resolution issues. What seems more likely to me is that the role of the posterior parietal cortex in motor adjustments is to be concerned with the current goal of the visuo-motor task, and to correct the motor plan in order to achieve the goal, regardless of the motor effector involved (or, better, with a very coarse somatotopy, given that posterior parietal control in these visuo-motor reaching and grasping tasks seems mainly contralateral).

But how can we reconcile this concept with the single-unit evidence of a discrete organization of posterior parietal areas concerned with specific effectors, such as LIP (eye), MIP (arm), AIP (finger)? One possibility is that the posterior parietal cortex allows the planning of actions from different effectors in a common frame of reference (Andersen, Snyder, Bradley, & Xing, 1997). However, it must be acknowledged that there is also neurophysiological evidence for a more distributed kind of processing in the posterior parietal cortex (Battaglia-Mayer et al., 2001; Johnson, Ferraina, Bianchi, & Caminiti, 1996; Marconi et al., 2001; Wise, Boussaud, Johnson, & Caminiti, 1997). Also, the role of the posterior parietal cortex in visuo-motor control should be interpreted in a larger network that includes other neural structures. In a positron emission tomography study adopting a task similar to the TMS study by Desmurget et al. (1999), the same group looked at blood flow changes while subjects either looked or looked and pointed with the right hand to stationary and non-stationary targets (Desmurget et al., 2001). Blood flow changes relative to updating the arm trajectory to compensate for the target jump were observed in the left posterior parietal cortex, the right cerebellum, and the left primary motor cortex. The interactions between the posterior parietal cortex and the cerebellum are important here. The cerebellum is thought to be critically associated with ‘internal models’, mimics of sensory-motor states that are useful for prediction (forward model) and control (inverse model) (Imamizu, Kuroda, Miyauchi, Yoshioka, & Kawato, 2003; Imamizu et al., 2000). Under conditions in which internal models are likely activated, the cerebellum and the posterior parietal cortex both increase their activity (Blakemore, Wolpert, & Frith, 1998). Computational considerations suggest that within the architecture of paired forward and inverse models there should be a 'responsibility signal' that assigns high or low priority to forward and inverse model pairs when facing specific sensory-motor contexts (Haruno, Wolpert, & Kawato, 2001). The role of the posterior parietal cortex in visuo-motor control may be that of generating a responsibility signal for internal model pairs in the cerebellum. The fact that TMS effect can be observed only at the beginning of the movement correction fits this hypothesis. Later stimulation would not be able to interfere with motor adjustment because, once selected, the forward–inverse model pair may run undisturbed in the cerebellum and send appropriate signals elsewhere.

5. Lateralization of posterior parietal cortex in visuo-motor behavior

Classical neurological observations have associated the posterior parietal cortex with striking lateralization patterns. Lesions in the left posterior parietal cortex are associated with apraxia, a higher order motor disorder, whereas lesions in the right posterior parietal cortex are associated with unilateral neglect, an attentional disorder (Heilman & Valenstein, 2003). Accordingly, recent TMS and fMRI studies have shown also striking lateralization patterns in healthy volunteers while performing visuo-motor tasks. In a study using repetitive TMS, healthy volunteers performed an orienting attention task and a motor attention task that required subjects to direct their attention to specific fingers of their hands that were subsequently used for motor response. TMS demonstrated that the right angular gyrus was critically associated with orienting attention, whereas the left supramarginal gyrus was critically associated with the motor attention task (Rushworth, Ellison, & Walsh, 2001a). A separate fMRI experiment by the same group also demonstrated a left posterior parietal mechanism for motor attention even when subjects only used their left hand (Rushworth, Krams, & Passingham, 2001b). This left lateralized posterior parietal mechanism for motor attention seems strongly tied with the left hemisphere network, including posterior parietal cortex, active during planning of familiar tool use (Johnson-Frey, Newman-Norlund, & Grafton, 2005). Planning of familiar tool use likely involves the retrieval of over-learned motor sequences of transitive actions—actions directed to objects. Lesions in the left posterior parietal cortex indeed produce praxis deficits, which may be manifested also during imitation. However, recent imaging work on imitation seems to show consistently right lateralized posterior parietal activations. This apparent inconsistency between lesion data and imaging of imitation is likely explained by the type of imitative actions used in lesion and imaging studies. The imaging data have focused on meaningless (thus definitely not over-learned) and intransitive actions, rather than familiar and transitive actions typically used in lesions studies, the most notable exception probably being some of the work of Goldenberg (Goldenberg, 1999, 2001; Goldenberg & Hagmann, 1997).

Imitation is a pervasive form of non-verbal social communication and learning during development, but also in adulthood (Hurley & Chater, 2005). It has been associated with the development of theory of mind and language and seems highly developed in humans (Hurley & Chater, 2005). My lab has been very active in recent years in the attempt to investigate the neural mechanisms of imitation and their links with the mirror neuron system, a fronto-parietal neural system in which neurons are active when an individual performs an action and when the same individual observes somebody else performing an action (Rizzolatti & Craighero, 2004). One finding that we have seen repeatedly (Iacoboni et al., 1999; Koski, Iacoboni, Dubeau, Woods, & Mazziotta, 2003) is that when healthy right handers use their dominant hand to imitate – as in a mirror, the left hand movement of somebody else – they activate their right (ipsilateral to the acting hand!) posterior parietal cortex. Imitating as in a mirror is the most 'natural' form of imitation, when the actor and the imitator are face to face, a rather typical situation in imitative behavior, the most common exception probably being dance teaching. The right posterior parietal activation during imitation, when compared to the left posterior parietal activation observed in motor attention and tool use tasks, suggests that – although all these tasks, because they all require visuo-motor transformations, they all must have something in common (the posterior parietal involvement being an index of such common denominator) – they also seem to have quite distinct properties, hence the contrasting lateralization patterns.

A possible explanation for the right posterior parietal lateralization observed in imitation tasks is the link between the mirror neuron system and self-recognition. In a recent study on self-recognition, healthy volunteers were asked to look at morphed faces composed of their own face and of the face of their best friend (the 'other'), and to detect whether the morph was composed more of self or other (Uddin, Kaplan, Molnar-Szakacs, Zaidel, & Iacoboni, 2005). Correct self-recognition was associated with activity in the right fronto-parietal mirror neuron system. This makes sense if one considers that the mirror neuron system maps the actions of others onto the motor repertoire of the self. When the self becomes an object of perception, the mapping process onto the perceiving self finds its best fit. More generally, these findings also fit an association between right posterior parietal cortex and self that has been suggested by several kinds of evidence (Blanke, Ortigue, Landis, & Seeck, 2002; Lou et al., 2004). Thus, when an eminently social visuo-motor task such as imitation automatically triggers representations of the self, the right posterior parietal cortex is activated. Planning the use of a tool is much less linked to self and social representations, and does not activate the right posterior parietal cortex. The left lateralized activity for tool use is likely linked to the sequential and hierarchical aspect of tool use motor behavior, sequencing and hierarchy being typically associated with left hemisphere functions, for instance language.

The left and right posterior parietal cortex are linked through robust callosal connections. In the last section of this paper, I will discuss some aspects of inter-hemispheric visuo-motor integration through callosal fibers of likely parietal origin.

6. Inter-hemispheric visuo-motor integration through posterior callosal fibers

The simplest visuo-motor task devised to study inter-hemispheric visuo-motor integration is what is called the Poffenberger paradigm (Poffenberger, 1912). Here, subjects respond with their left and their right hand to unpatterned light flashes that are lateralized to the left and the right visual hemi-field. In this task, there are no catch trials and there is no response selection, given that during a block of trials subjects are told to use only one of the two hands and to respond as fast as possible whenever a light flash is presented. The rationale behind the task is that when subjects respond with the hand ipsilateral to the light flash (this is called the Uncrossed condition), there is no need to transfer information from one hemisphere to the other, since in the Uncrossed condition the same hemisphere receives the visual input and controls the motor output. On the other hand, when subjects respond with the hand contralateral to the light flash (this is called the Crossed condition), the visuo-motor integration process must involve both hemispheres since the hemisphere that receives the visual input is not the one that controls the motor output. Indeed, reaction times in the Crossed condition are on average slower than reaction times in the Uncrossed condition, and the so-called Crossed–Uncrossed Difference (CUD) is taken to reflect the delay that occurs through callosal fibers to allow inert-hemispheric visuo-motor integration.

A series of behavioral studies have investigated the functional level of the inter-hemispheric visuo-motor transfer. Early studies, manipulating the visual parameters of the light flashes (i.e., brightness and eccentricity) in healthy volunteers found no effects on the CUD and concluded that the transfer could not be visual (Berlucchi, Heron, Hyman, Rizzolatti, & Umiltá, 1971). A later study manipulated systematically visual and motor parameters and while replicating the absence of CUD effects for visual manipulation, reported reliable CUD changes during manipulation of motor response parameters. These effects were observed in healthy volunteers but not in split-brain patients (Iacoboni & Zaidel, 1995). Taken together, these data suggested that the inter-hemispheric visuo-motor integration process occurred at a motor level, and through callosal fibers. Findings on a patient tested before and after a partial callosotomy sparing the splenium of the corpus callosum, where visual fibers are grouped (Zaidel & Iacoboni, 2003), helped in refining this concept. In fact, in this patient no effects of visual manipulation on the CUD were observed before the surgery, in line with previous findings. However, after the callosotomy, retinal eccentricity manipulation did affect the CUD, suggesting that both visual and motor transfer can occur, but that in the healthy brain the motor transfer dominates, probably because it is faster than the visual one.

A recent fMRI study has looked into the functional anatomy of the visuo-motor transformations required by the Poffenberger paradigm. When the Uncrossed conditions were subtracted from the Crossed conditions, reliably higher BOLD signal was observed in bilateral prefrontal, bilateral premotor, and right superior parietal cortex (Iacoboni & Zaidel, 2004). When the individual CUDs of the participants were correlated with signal intensity changes, a strong correlation emerged between CUD and superior parietal cortex, thus suggesting that activity in this area is more strongly linked with the behavioral results. Given that the previous behavioral studies had indicated that the dominant functional level of the transfer is ‘motor’, it is likely also that the functional significance of the superior parietal area is more ‘motor’ than ‘visual’. To better understand the functional aspects of the inter-hemispheric visuo-motor integration implemented by this superior parietal area and the callosal fibers originating from it, it is useful to discuss some chronometric and single-unit findings. In a behavioral study in which stop trials were intermixed with ‘go’ trials in an otherwise typical Poffenberger paradigm, subjects were better able to refrain from responding when the stop signal occurred during the Crossed condition (Cavina-Pratesi, Bricolo, Pellegrini, & Marzi, 2004). This suggested that what is transferred can be controlled, a concept that fits well the evidence for visuo-motor control associated with the superior parietal cortex. Moreover, single-unit data from ‘go no-go’ tasks show that neuronal firing in superior parietal neurons is associated with the intention to respond during no-go trials (Kalaska & Crammond, 1995). It seems likely, then, that what is transferred during the Poffenberger paradigm by callosal fibers originating from the superior parietal cortex is the ‘intention to respond’. This concept also fits well with concepts derived from neurophysiological evidence and linking the posterior parietal cortex to motor intentions (Snyder et al., 1997).

7. Conclusion

Visuo-motor integration and control is a pervasive aspect of human behavior and the posterior parietal cortex is a critical structure associated with it. The main concepts I addressed in this paper can be summarized in four major points: first, in spite of its large expansion, the human posterior parietal cortex has preserved the internal structure of the posterior parietal cortex of other primates; second, visuo-motor control in the posterior parietal cortex is likely implemented through the selection and de-selection of internal models represented elsewhere (definitely in the cerebellum, but likely not only in the cerebellum); third, lateralization of visuo-motor functions in the posterior parietal cortex suggests that the left posterior parietal cortex is more concerned with tool use and the right posterior parietal cortex is more concerned with imitation of the actions of others; fourth, visuo-motor inter-hemispheric transfer through parietal callosal fibers seems to occur at the level of ‘motor intention’.

Although these are still relatively sketchy concepts that require development and refinement, they have the merit of being able to generate tractable problems that can be tested by future studies.

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