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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'.

Keywords: Imitation; Internal models; Interhemispheric transfer; Self; Lateralization

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).