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Parietal modules for reaching

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ABSTRACT

Optic ataxia (OA) is classically defined as a deficit of visually guided movements that follows lesions of the posterior part of the posterior parietal cortex (PPC). Since the formalisation of the double stream of visual information processing [Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press] and the use of OA as an argument in favour of the involvement of the posterior parietal cortex (dorsal stream) in visually guided movements, many studies have looked at the visuomotor deficits of these patients. In parallel, the development of neuroimaging methods have led to increasing information about the role of the posterior parietal cortex in visually guided actions. In this article, we discuss the similarities and differences in the results that emerged from these two complementary viewpoints by combining a meta-analysis of neuroimaging data on reaching with lesion studies from OA patients and results of our own fMRI study on reaching in the ipsi- and contra-lateral visual field. We identified four bilateral parietal foci from the meta-analysis and found that the more posterior foci showed greater lateralisation for contralateral visual stimulation than more anterior ones Additionally, the more anterior foci showed greater lateralisation for the use of the contralateral hand than the more posterior ones. Therefore, we can demonstrate that they are organised along a postero-anterior gradient of visual-to-somatic information integration. Furthermore, from the combination of imaging and lesion data it can be inferred that a lesion of the three most posterior foci responsible for the target-hand integration could explain the hand and field effect revealed in OA reaching behaviour.

1. Introduction

Bálint (1909) described a patient with a large bilateral lesion in the posterior parietal cortex (PPC) who exhibited a particular pattern of deficits (the Bálint syndrome), including reaching inaccuracy (Hecaen & De Ajuriaguerra, 1954). One of the first studies that isolated optic ataxia (OA) (ataxie optique) from the Bálint syndrome was from Garcin, Rondot and de Recondo (1967). He described pure cases of unilateral lesion patients showing reaching deficits only in peripheral vision and without any other primary sensory or motor deficit, neglect or apraxia. The interpretation of OA as a specific visuomotor deficit has been reinforced by the careful study of Vighetto in the 80s (Perenin & Vighetto, 1983, 1988). He notably showed that reaching errors of unilateral patients depended both on the use of the contralesional hand in both visual fields (hand effect) and on the presentation of the target in the contralesional field (field effect). This combination of sensory and motor influences, as well as the location of the PPC lying between the visual and the motor cortices support the idea that the OA deficit affects the visuomotor interface. This interpretation of OA was one of the arguments used by Milner and Goodale (1995) to change the interpretation of the function of the dorsal stream from "where" to "how". Their model of the double stream of visual information processing has been one of the most influential in modern cognitive sciences and therefore has increased interest in OA. In parallel, the development of neuroimaging techniques, especially functional magnetic resonance imaging (fMRI), has been applied in the field of visually guided movement despite difficult technical matters.

Neuroimaging investigates the neuronal correlates of a function in the normal brain. New methods are now beginning to emerge for more comprehensive analysis of fMRI data. However, it is often difficult to assess the specific role of each region from the usually obtained patterns of activation and to identify the necessary anatomical component(s) and connections that sustain the studied function. Neuropsychology on the other hand, allows the identification of deficits related to a damaged brain region but with

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no precise anatomical definition. Also, the consequences of the recovery mechanisms are difficult to assess. Therefore, the cross-comparison of these methods may allow us to validate findings concerning characteristics of the sensorimotor function. After first reviewing the main paradigm differences between neuroimaging and neuropsychology, we will identify the main parietal foci activated during a reaching task in fMRI or PET studies by means of a meta-analysis. Then, we will present fMRI data from a study suitably designed to further test the emerging foci for their role as an interface of vision and motor integration. Finally, we will review the main results coming from OA patient studies and compare these results with what has been found in fMRI experiments. The main focus of our polymodal approach is to provide further evidence for a fronto-parietal gradient of visuomotor information processing and to identify parietal regions involved in the processing of hand effect and field effect in analogy to OA.

2. Paradigm differences between neuroimaging and patient studies

Due to the technical limits imposed by the MRI machine, most fMRI studies claiming to investigate brain activity related to reaching have not used proper reaching movement. Instead, the subjects were asked to orient their wrist in order to point with their index finger in direction of the target (e.g. Astafiev et al., 2003; Connolly, Goodale, DeSouza, Menon, & Vilis, 2000; Connolly, Andersen, & Goodale, 2003; Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002). In this case, only the direction of the target has to be computed but not its exact spatial position. Some studies have even used a joystick to get spatially oriented movements (e.g. Oreja-Guevara et al., 2004). We can question the degree to which the results of studies which use such ecologically invalid movements are able to reveal neural structures involved in reaching.

In the same vein, in fMRI, because the subjects are lying supine in the scanner, the target presentation is a real problem. Most of the time, it is resolved by using a mirror fixed to the head coil that reflects the image of the visual target (e.g. Astafiev et al., 2003). However, this induces a dissociation between the space in which the movement is performed and where the target is presented. Some recent studies have chosen to tilt the subjects head in the MRI coil (Prado et al., 2005) or to tilt the head and the torso (Beurze, de Lange, Toni, & Medendorp, 2007) in order to have a direct view of the target and to be able to fit the movement direction to the actual target position. The matter of the mirror is important because it induces extra spatial transformations that also cause activation in the PPC. In a PET study, Binkofski et al. (2003) directly compared the brain activation induced by reaching to a visual target while directly viewing the scene or by looking at the target through a mirror. They showed that pre-motor and posterior parietal areas are additionally activated in the mirror condition. These areas are the ones primary activated in any reaching task. Furthermore, Binkofski, Buccino, Dohle, Seitz, and Freund (1999) and Binkofski et al. (2003) have isolated a specific neurological disorder called mirror ataxia. This pathology is characterised by pronounced mis-reaching towards objects that are presented through a mirror (Binkofski et al., 1999). Such patients are unable to operate in the mirrored space, and need considerable corrections to be able to grasp the object. Interestingly, most of these patients do not present OA. Mirror ataxia seems to rely on a different lesion site, the anterior part of the IPL. These observations raise a fundamental question about the use of a mirror to present targets in fMRI studies.

Another striking example of differences between paradigms used in fMRI and in behavioural patient studies is linked to one of the most counter-intuitive results of OA experiments. It is the effect of a delay between the target presentation and the movement execution. Whereas control subjects' behaviour in such condition is worse than in immediate pointing, patients with OA are more accurate when they reach toward a memorised target (Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999; Milner et al., 2001; Rossetti et al., 2005). The authors explain this phenomenon by the existence of an additional pathway for visually guided action based on memorised position which could be the ventral pathway instead of the dorsal one used for immediate pointing. This idea has been reinforced by studies of a visual agnosia patient (DF) who showed the reverse pattern of behaviour, i.e. her reaching capacities which are not impaired in the normal condition are drastically low in the delayed condition (Milner et al., 1999). However, to minimise the effect of the movement that causes artefacts in the scanner, and to concentrate on the planning part of the action, many fMRI experiments have added a delay between the target presentation and the movement execution (e.g. Medendorp, Goltz, Crawford, & Vilis, 2004; Connolly et al., 2003). Interestingly, neuroimaging experiments do not show a shift from the involvement of the dorsal stream to the ventral stream in the delayed condition but still show activation in the parietal areas. But no study has directly asked any of these questions; therefore we still cannot determine the effect of these paradigm differences based on previous studies.

Table 1
List of the articles used for the meta-analysis. The information given concerns the type of imaging method (PET or fMRI), the type of movement (point = rotation of the wrist, reach = rotation of the elbow), the type of target presentation and if a delay was introduced between the target presentation and the execution of the movement.

Blangero et al. (unpublished)	fMRI	Reach	No mirror	No delay
Filimon, Nelson, Hagler, and Sereno (2007)	fMRI	Reach	No mirror	No delay
Beurze et al. (2007)	fMRI	Reach	No mirror	Delay
Prado et al. (2005)	fMRI	Reach	No mirror	No delay
Oreja-Guevara et al. (2004)	fMRI	Joystick	Mirror	No delay
Astafiev et al. (2003)	fMRI	Point	Mirror	Delay
Simon et al. (2002)	fMRI	Point	Mirror	No delay
de Jong, van der Graaf, and Paans (2001)	PET	Reach	No mirror	No delay
Desmurget et al. (2001)	PET	Reach	No mirror	No delay
Connolly et al. (2000)	fMRI	Point	No mirror	No delay
Inoue et al. (1998)	PET	Reach	Video	No delay
Kertzman et al. (1997)	PET	Reach	No mirror	No delay
Grafton et al. (1996)	PET	Reach	No mirror	No delay

3. Reaching: a meta-analysis of neuroimaging studies

As highlighted above, the neuroimaging studies investigating reaching are using different paradigms. Furthermore, depending on the chosen contrasts and control conditions, the results obtained can differ considerably. For example, a large number of different parietal activation coordinates have been reported in the literature (Fig. 1A), thus it could be interesting to know if these represent different foci or if they can be grouped into clusters to isolate the main areas. A way to get the pertinent network involved in a specific function while ignoring the inherent experimental differences is to realise a function-location meta-analysis. A popular method to realise statistically relevant meta-analysis is activation likelihood estimation (ALE). This method was initially developed by Turkeltaub, Eden, Jones, and Zeffiro (2002) and was integrated, after some modifications (Laird et al., 2005), to an application called GingerALE (http://www.brainmap.org/ale/index.html), which is part of the BrainMap software. We used this method to investigate the reaching network that is the most reliable independent of inter-study differences (Fig. 1B). The meta-analysis is based on 12 papers studying reaching as well as recent data of our own (Table 1). We excluded studies of other type of movements (like grasping) and only included studies that published the whole brain activations and not only the region of interests' coordinates. There are five PET and eight fMRI studies. Most of the peak activations were in Talairach coordinates, which is the reference used by the Gin-