

Posterior parietal cortex control of reach-to-grasp movements in humans

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Abstract

The aim of the present study was to ascertain the neural correlates for the integration of visual information with the control of the reach-to-grasp action in the healthy human brain. Nine adult subjects (18–38 years; four females and five males) were scanned using functional magnetic resonance imaging while reaching-to-grasp a three-dimensional target. Results demonstrated differential activation of the parietal cortices according to the number of potential targets to be taken into account before movement initiation and the variability of target location. Comparing conditions where a target object that can appear at an unpredictable location with conditions where the target object appears at a predictable location revealed activations in the left superior parietal lobule, the left parieto-occipital sulcus and the right intraparietal sulcus. Results are discussed in terms of visual selective attention and action planning.

Introduction

From everyday experience, we intuitively know that we carry out many visually guided actions on the objects that surround us. For example, when choosing a piece of fruit from a bowl, many fruits are visible and within reach, but only the one that we would like to pick up governs the particular pattern and direction of movement. Although this action seems simple enough, the processes involved are complex. We need to use visual information to guide these reach-to-grasp actions.

Over the past 20 years a considerable amount of work has been carried out into understanding the first part of the process, how visual information is used in reach-to-grasp actions (Jeannerod, 1988, 1997 for review). However much less work has been conducted into the factors that determine the processes of response selection behind the visual perception systems for the control of action.

From neurophysiology in primates and neuropsychology in humans the parietal cortices have been identified as regions that are vital for many functions including those necessary to perform an action. Single-cell recordings have shown that the posterior parietal lobe is a mosaic of areas fundamental for the transformation of sensory information into information for action (see Rizzolatti *et al.*, 1997 for review). For instance, neurons matching the perceived depth structure of an object with grasping movements directed towards the object have been found in the lateral bank of the intraparietal sulcus (Sakata & Taira, 1994). Neurons concerned with the execution and the preparation of reaching movements have been found within the anterior bank of the parieto-occipital sulcus (Fattori *et al.*, 2001; Marconi *et al.*, 2001).

Along these lines, in humans, the intraparietal and superior parietal cortices have been shown to be important for the visual control of action (Milner & Goodale, 1995). Lesions centred in the intraparietal sulcus and adjacent superior parietal lobule cause optic ataxia, that is, disordered visual control of the arm, hand and fingers (Perenin & Vighetto, 1988). This set of deficits is strikingly similar to that seen in monkeys. Furthermore, functional imaging studies tell a similar story. Grafton *et al.* (1996) demonstrated superior parietal lobe activation during the performance of both visually guided reaching and visually guided grasping tasks. Faillenot *et al.* (1997) found activation in the posterior parietal cortex when subjects were instructed to accurately grasp the object and Binkofsky *et al.* (1998) showed a specific activation of the anterior lateral bank of the intraparietal sulcus during grasping. Evidence from animal lesion studies thus converges with neuropsychological and functional imaging data in suggesting the posterior parietal cortex as the locus in the brain where sensory information is also used for motor actions.

The aim of the present experiment was to use functional magnetic resonance imaging (fMRI) to map those areas in the human brain that are involved in sensorimotor integration. We asked subjects to reach-to-grasp three-dimensional (3-D) objects whilst being scanned for functional activations. By presenting a target that could appear at predictable or unpredictable locations, we challenged the parietal action system to identify regions concerned with the planning of arm and hand movements. This allowed us to perform an analysis comparing the preparation for an action when the target's location is unpredictable with preparation for an action when the target's location is predictable. In doing this we were able to tell whether the control of the reach-to-grasp action is anatomically subdivided within the human parietal cortex, and also whether activity within the parietal cortex is modulated depending on whether potential targets

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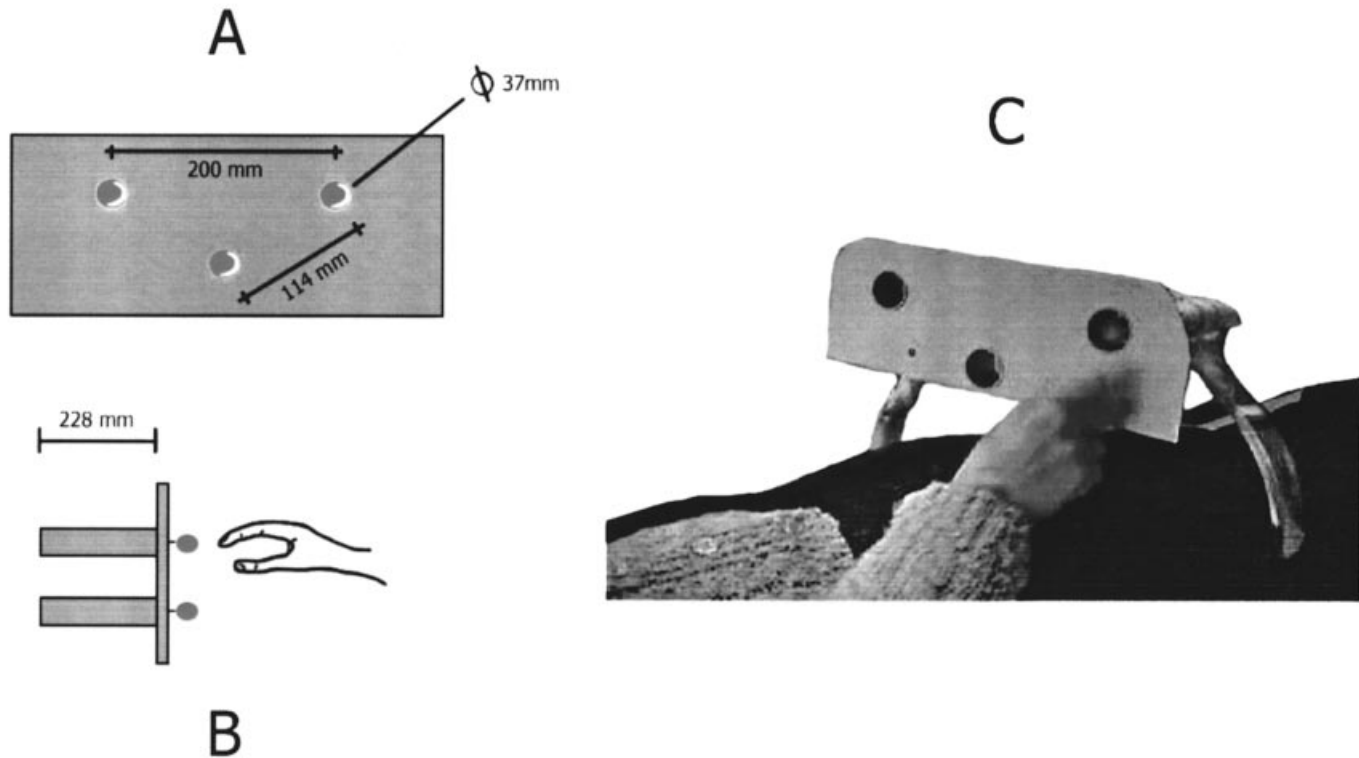


FIG. 1. Experimental apparatus. (A) The front view of the apparatus, (B) the lateral view of the apparatus and (C) the position of the subject and the position of the apparatus within the scanner.

appear at one or more than one target location. Some of these results have been published in abstract form (Chapman *et al.*, 2001).

Materials and methods

Subjects

Nine healthy adults (four females, five males; age 18–38 years) participated in the experiment. All subjects had normal vision, were right-handed and had normal neurological and psychiatric histories. Ethical approval was given by the Ethics Committees of the Howard Florey Institute and the University of Melbourne. The subjects gave their informed consent in writing.

Data acquisition

The functional scans were acquired using a 1.5T General Electric scanner (Echospeed, Waukesha, WI, USA) with echo planar imaging [sequence repetition time (TR) = 3500 ms, signal-(echo-)gathering time (TE) = 40 ms, flip angle (FA) = 60, matrix = 64×64]. Fifteen contiguous 7 mm thick transaxial slices with a 260 mm field of view (FOV) were obtained, yielding a voxel size of $4 \times 4 \times 7 \text{ mm}^3$. With 32 whole brain volumes acquired for each experimental run a total of 256 (eight acquisitions) functional images were obtained for each subject. Prior to functional imaging, a high resolution 3-D FAST spoiled gradient echo T1 with an inversion time of 300 ms [field of view (FOV) = 260 mm, FA = 25, matrix = 256×224 , 1.5 mm slice thickness, IR prep SPGR] was acquired sagittally.

Stimuli

To investigate reach-to-grasp movements towards 3-D stimuli a pneumatic apparatus was designed (see Figs 1 and 2). The apparatus allowed the experimenter to control for stimuli visibility. The stimuli

consisted of three red balls (each 15 mm in diameter) that were encased within three barrels (37 mm in diameter and 228 mm in length), which were in turn situated behind a plastic mounting panel. Distances between the barrels carrying the stimuli were as follows: 114 mm between the middle and right barrels; 114 mm between the middle and left barrels; and 200 mm between the left and right barrels. The middle barrel was vertically offset 52 mm below the left and right barrels. The face of the apparatus was mounted on an arch of plastic and placed over the subject's body around the upper thigh region in order to minimize arm movement. Each barrel was attached to an 8 m length of pneumatic tubing and all three lengths of tubing were connected to a computerized control system that regulated the compressed medical air supply (maximum pressure 137 kPa) to the apparatus. The delay between the input for stimulus appearance and the actual appearance of the stimulus was 50 ms.

The apparatus worked as follows: the balls extended out of the barrels on the end of pneumatic pistons; the pistons extended to allow the balls to be grasped using a precision grip consisting of the opposition between the index finger and the thumb of the right hand; the pistons were spring-loaded so that after such action was performed stimuli retracted into the barrels.

Task

The subjects were told prior to the start of the practice session that any combination of one, two or three stimuli would emerge from the display. There were five conditions: (i) three stimuli condition; (ii) two stimuli condition; (iii) one stimulus, three possible locations condition; (iv) one stimulus one location condition; (v) view condition. Subjects were instructed to reach-to-grasp (but not hold) the designated target stimulus using only their right-hand thumb and index finger (Fig. 1).

Each trial was repeated seven times over a 10.5 s condition period (1.5 s inter-stimulus interval) and the five conditions were presented randomly without replacement within a scanning block. Two experimental blocks were presented per MR acquisition sequence with a total run time of 107 s. All subjects were given a practice response period that included at least four blocks of trials with each block containing all five conditions.

Three stimuli condition

During this condition all three stimuli appeared for 250 ms, after which two stimuli retracted into the apparatus and the remaining stimulus became the target. Subjects had 1 s to reach-to-grasp the target, which then retracted into the barrel. The final component of this condition was a 250 ms period where no stimuli appeared in preparation for the next trial.

Two stimuli condition

Random combinations of two stimuli (left and middle, left and right, or right and middle) were initially presented for 250 ms. One ball was then retracted; thus the remaining ball became the target. Subjects had 1 s to reach-to-grasp the target, which subsequently retracted into the apparatus. This was followed by a 250 ms blank display period (without any stimuli), again included to clear the display for the next trial.

One stimulus three possible locations condition

During this condition one stimulus appeared at any of the three locations (left, right or middle) for 1 s. The location sequence was randomized *within* the condition period and the likelihood of the target appearing at any of the three locations was equal. Subjects had 1 s to reach-to-grasp the target, which then retracted into the apparatus. Finally, a blank display (without any stimuli) appeared for 500 ms; this period was included to clear the display for the next trial.

One stimulus one location condition

During this condition one stimulus appeared at one of the three locations (left, right or middle) for 1 s. The initial choice of location for the target was randomized, but within a condition period the target always appeared at the same location. Following the appearance of the target, subjects had 1 s to reach-to-grasp the target, which then retracted into the apparatus. The final component of this condition was a blank display (500 ms), required, as previously mentioned, to clear the display for the next trial. The distinction between this condition and the one stimulus three possible locations condition described previously is important. In the latter the target could appear at any of the three locations within a single condition period, in the former, the target appeared continuously at the same location during a condition period (although the target's location was varied across the experiment).

View condition

In this condition all three stimuli remained retracted within the barrels for the entire condition period. No motor response from the subjects was required.

Baseline

Several of the above mentioned conditions were used as baselines. In order to establish contralateral motor activity, the view condition, where three stationary stimuli were presented was used as a baseline for all other conditions. In order to look more specifically at a

network subserving sensorimotor integration, all conditions with more than one stimulus were examined with the one stimulus one location condition. To examine the effect of changing target location we compared the one stimulus three possible locations condition with the one stimulus one location condition. In addition, the effect of multiple stimuli was investigated by comparing the three stimuli condition with the one stimulus three possible locations condition.

Analysis

The fMRI analysis was carried out on the group of nine subjects using SPM99 (Friston *et al.*, 1995). Each individual functional data set was aligned to the corresponding individual's anatomical image. Each subject's data set was then spatially normalized into Talairach (Talairach & Tournoux, 1988) standard space using AIR3.08 (Woods *et al.*, 1998). Prior to fixed effects analysis, images were smoothed ($4 \times 4 \times 7 \text{ mm}^3$), globally normalized with proportional scaling, and a hi-pass filter was applied. Corrections for multiple comparisons based on the random field theory were also applied. Single subtraction contrasts were computed using SPM99 to identify differences in activations between the five conditions. These group activation results were overlaid onto the group average structural MR image.

Head movement was estimated using the 6 degrees of freedom rigid body realignment algorithm implemented in SPM99. To test for motion-induced activation, motion parameters were included as confounds in an analysis of the subject with the greatest head movement but no changes were observed in the original activation map. Based on this finding, no correction for motion (using motion parameters as confounds) was included in the final statistical analyses.

Results

In this paper we have focused on three experimental comparisons: the three stimuli condition compared with the one stimulus one location condition; the three stimuli condition compared with the one stimulus three possible locations condition; and the one stimulus three possible locations condition compared with the one stimulus one location condition. A pictorial representation of all three comparisons can be seen in Figure 2 with the results of these comparisons given in Table 1.

The three stimuli condition *minus* the one stimulus one location condition (Fig. 2A) produced contralateral activations in the parieto-occipital (PO) sulcus and superior parietal lobe (SPL). Ipsilateral activations were found in the intraparietal sulcus (IPs), the pre-motor and the inferior occipital cortical areas.

The three stimuli condition *minus* the one stimulus three possible locations condition produced activation in the left PO sulcus as well as a right IPs activation (Fig. 2B).

Activations in the left SPL region and the right IPs were found to be present when subtracting the condition where the stimulus appeared at a fixed location from the condition where one stimulus appeared at one of the three possible locations (see Fig. 2C).

Discussion

The aim of the present work was to identify neural substrates for the visual control of action in healthy adult humans. The hypothesis that parietal regions activate differentially according to the number of potential target locations was confirmed.

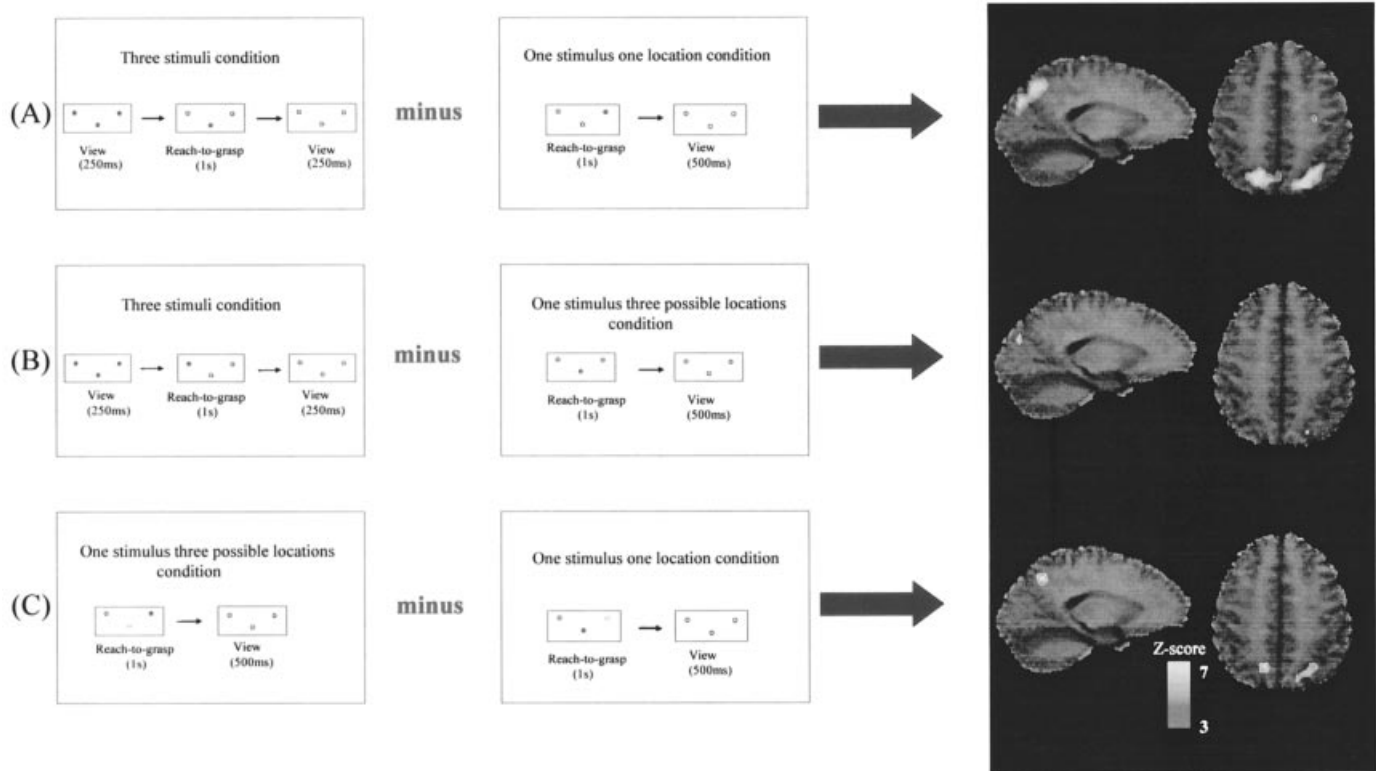


FIG. 2. (A) Brain activation associated with changing target location and the number of visual stimuli presented before movement initiation. The comparison here is between the three stimuli condition and the one stimulus one location condition. (B) The effect of presenting three stimuli before movement initiation. The comparison here is between the three stimuli condition and the one stimulus three possible locations condition. (C) The effect of changing target location. The comparison here is between the one stimulus three possible locations condition and the one stimulus one location condition. Please note that the red dots symbolize the stimuli, whereas the empty circles represent the locations where the stimuli that do not become targets are hidden. (All sagittal sections shown are within the left hemisphere).

We found an increased activation in the left SPL, the left PO sulcus and the right IPs when comparing a condition where the target location was unpredictable (three stimuli condition) with a condition where the target was presented at a predictable location (one stimulus one location condition). One potential explanation for the extra activation in the three stimuli condition might be related to the extra visual selection requirements relative to when only one location is monitored. Corbetta *et al.* (1993) studied regions of the human brain related to the orienting of attention to different locations in the visual field. In particular, when comparing conditions where subjects were required to shift visual attention to cued locations with a condition where attention was maintained centrally during the presentation of peripheral stimuli, bilateral SPL activations were identified. To account for their results these authors proposed that the SPL might work to coordinate the focus of processing to locations and objects via a 'spatial shifter mechanism'.

So it is therefore possible that the increased SPL activation found in the present study could reflect extra location monitoring/selection requirements in order for the 'spatial shifter mechanism' to direct the focus of processing to the selected stimulus for the response. This interpretation makes most sense when considering the differential left SPL activity observed in this study during a comparison between the condition where one target appeared at unpredictable locations with the condition where one target appeared in a single location. It is in this comparison that neural processes associated with such a 'spatial shifter mechanism' would most likely be elicited.

However, in contrast to the findings of Corbetta *et al.* (1993) we found that the increase in SPL activation was not bilateral but confined to the left hemisphere. A possible explanation for this effect comes from recent studies that have extended the notion of orienting of attention not only to processes concerned with orienting or eye movements but also to an analogous process defined as motor attention associated with the preparation of limb movements (Deiber *et al.*, 1996; Rushworth *et al.*, 1997, 2001; Krams *et al.*, 1998; Castiello & Paine, 2002). The region thought to be responsible for 'motor attention' is located within the left parietal areas. Given the nature of our tasks the increasing need for selection may correspond to an increase in motor attentional demand within the left SPL. This could mean that the proposed 'spatial shifter mechanism' is present bilaterally, but depending on the task, the right or the left parietal areas are differentially activated.

Another area that activated differentially when comparing predictable vs. unpredictable target locations was the left PO sulcus. In this case it also appears that the attentional state of the observer can modulate preparatory activity in this region. When three stimuli are being monitored, visual attention is most likely to be spread across the field to monitor for all potential targets and would be sustained for the period of time prior to motor response. In other words, the additional function in the three stimuli condition may be attributed to the extra attention required when monitoring three potential target locations prior to movement initiation. However, it is also possible that the former preparatory sensory influences play some role in modulating the sensory response to the incoming stimulus that is

TABLE 1. Brain activation for three contrasts

Contrast/Region	BA	(x, y, z)	Cluster size	$P_{(\text{corrected})}$	Z-score
First contrast (three-stimuli condition minus one-stimulus one-location condition)					
L PO sulcus	19	(-16, -80, 36)	(676)*	< 0.001	7.62
L SP cortex	7	(-18, -68, 48)	(676)*	< 0.001	7.32
	7	(-8, -66, 52)	(676)*	< 0.001	6.87
R parietal cortex	7	(22, -68, 52)	779	< 0.001	∞
R pre-motor cortex	6	(36, -8, 60)	103	< 0.005	5.18
R inferior occipital cortex	17	(10, -76, 8)	313	< 0.001	6.58
Second contrast (three-stimuli condition minus one-stimulus, three-possible-locations condition)					
L PO sulcus	19	(-16, -80, 36)	50	< 0.016	4.94
R parietal cortex	7	(22, -70, 52)	52	< 0.025	4.84
Third contrast (one-stimulus, three-possible-locations condition minus one-stimulus one-location condition)					
L SP cortex	7	(-18, -68, 48)	(471)**	< 0.001	5.76
	7	(-36, -54, 52)	(471)**	< 0.051	4.67
R parietal cortex	7	(24, -66, 52)	371	< 0.001	5.68

*At $P_{(\text{corrected})} < 0.001$, the combined left occipital and parietal activations have a total of cluster size of 676 voxels. **At $P_{(\text{corrected})} < 0.001$, the combined left parietal activations have a total of cluster size of 471 voxels. PO, parietal-occipital; SP, superior parietal; R, right; L, left.

linked to a specific response. In connection with this, monkey studies have suggested that regions in the PO sulcus are well situated as an early 'node' of a network mediating visually guided reaching (Caminiti *et al.*, 1999). More recently, Fattori *et al.* (2001) discovered neurons in area V6A (found within the anterior bank of the PO sulcus) that discharge during the preparation of arm movements and are direction-selective. In our study, the simultaneous presentation of more than one potential target (at three separate locations) could place an increased demand on the reaching preparation processes. Consequently the activation in the left PO sulcus may signify that in circumstances where selection and motor planning might be more demanding, the activity for two different but not necessarily unrelated functions – namely motor planning and visual attention – is increased.

In support of the idea for a coexistence within a single parietal region of visual attention and visuomotor mechanisms, we found that the right IPs was a region that differentially activated when manipulating the number of visual stimuli before movement initiation. It is well known that in humans damage in this superior parietal region causes various visuomotor disorders, including optic ataxia (Perenin & Vighetto, 1988). Furthermore, it is also known that attentional modulation effects can be observed in approximately the same region in human subjects. Corbetta *et al.* (1993) have shown in a positron emission tomography study that cerebral flow selectively increases in this location in association with selective visuospatial attention. Thus, although a contributing factor to account for at least part of the right IPs activation could be the greater visual attention requirement during the three stimuli condition, a possible role for the IPs during action preparation cannot be discarded. Two pieces of evidence support this hypothesis. First, Sakata *et al.* (1997) have identified a concentration of cells in the lateral bank of the IPs that they determined to be of importance for the identification of the 3-D shape of objects. Thus, it might be proposed that the initial monitoring by the subject of three objects to be potentially acted upon places substantial requirements on the neural system concerned with the coding of object properties for the purpose of action. Second, the lateral intraparietal area of a monkey's brain contains cells that fire before either saccades, arm reaches (Snyder *et al.*, 1997) or hand manipulation (Murata *et al.*, 1996). Furthermore, as suggested by Binkofsky *et al.* (1998), the human homologue of the anterior intraparietal area mediates the processing of sensorimotor integration of finger movements.

One final issue concerns the ipsilateral nature of the right IPs activation. Mattay *et al.* (1998) found that the automaticity of a task differentially activated the parietal cortex. When the task had an unknown element or was less automatic (e.g. random finger movements) enhanced ipsilateral activity was observed in this region. The low level of automaticity that characterizes the present task might thus be responsible for the ipsilateral pattern of activity observed in all of our comparisons.

In conclusion the present study confirms and extends previous findings that have put forward the notion that visual selection and action planning mechanisms are processes distributed and modulated within and over different parietal areas spanning from the SPL to the adjacent parts of the IPs.

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Abbreviations

3-D, three-dimensional; FA, flip angle; fMRI, functional magnetic resonance imaging; FOV, field of view; IPs, intraparietal sulcus; MR, magnetic resonance; PO, parietal-occipital; SPL, superior parietal lobe; TE, signal-(echo-)gathering time; TR, sequence repetition time.

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