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Differential cortical activity for precision and whole-hand visually guided grasping in humans

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Abstract

Effective grasping involves the remarkable ability to implement multiple grasp configurations such as precision grip (PG; opposition between the index finger and thumb) and whole-hand grasp (WHG), depending on the properties of the object grasped (e.g. size, shape and weight). In the monkey brain, different groups of cells in the anterior–lateral bank of the intraparietal sulcus (area AIP) are differentially active for various hand configurations during grasping of differently shaped objects. Visually guided grasping studies in humans suggest the anterior intraparietal sulcus (aIPS) as the homologue of macaque area AIP, but leave unresolved the question of whether activity in human aIPS reflects the relationship between object size and grasp configuration, as in macaques. To address this issue, a human fMRI study was conducted in which objects were grasped with the right hand while object size was varied. The results indicated that the left aIPS was active when the subjects naturally adopted a PG to grasp the small object but showed a much weaker response when subjects naturally adopted a WHG to grasp the large object. The primary motor cortex and somatosensory cortices were active for both PG and WHG. Our results suggest that, in humans, the aIPS is centrally involved in determining the type of grasp.

Introduction

Monkey single-unit recording studies implicate a region along the anterior–lateral bank of the intraparietal sulcus (area AIP) for controlling grasping movements (Taira *et al*., 1990; Gallese *et al*., 1994; Sakata *et al*., 1995; Murata *et al*., 2000). Neurons in AIP are recruited for visual object discrimination and are activated for specific hand configurations during grasping of differently shaped objects. The causal involvement of AIP in grasp has also been demonstrated through pharmacological inactivation of this area with consequent disruption of hand preshaping during grasping (Gallese *et al*., 1994).

In humans, a grasp-specific region within the anterior intraparietal sulcus (aIPS) has been proposed as the putative homolog of macaque area AIP. Patients with circumscribed lesions to the aIPS show marked deficits in hand preshaping during visually guided reach-to-grasp movements, whereas reaching remains relatively intact (Binkofski *et al*., 1998). Several functional neuroimaging studies indicate that focal activation within the aIPS of the healthy brain occurs in association with visually guided grasping (Binkofski *et al*., 1998, 1999; Culham *et al*., 2003, 2004; Frey *et al*., 2005). However, although these studies varied the size and shape of the objects, participants were required to use a precision grip (PG) in all cases (Binkofski *et al*., 1998; Culham *et al*., 2003, 2004; Frey *et al*., 2005). Those that did ask participants to perform a specific type of grasp [i.e. PG or whole-hand grasp (WHG)], related to the size of the to-be-grasped object, considered only nonvisually guided isometric grip tasks (Ehrsson *et al*., 2000; Grèzes *et al*., 2003) or did not report separate data for different types of grasp (Grèzes *et al*., 2003). Therefore the above studies do not test for the matching of grasp type to object size that is implemented in primate aIPS. Furthermore, they may not be comparable with previous behavioural and neurophysiological studies in which specific kinematic patterns and neural activations for grasping of differently shaped objects have been identified (for review see Castiello, 2005). Therefore the question of how human aIPS responds to different grasp configurations has yet to be addressed.

In the present paper, we measured aIPS responses for two types of grasp related to different-sized objects in human volunteers using functional magnetic resonance imaging (fMRI). We designed two closely matched grasping tasks in which participants had to perform a reach-to-grasp action towards a small object requiring a PG or a large object requiring a WHG. Measuring the strength of the aIPS response in the two grasping conditions enabled us to test whether human aIPS activity was modulated by grasp type.

Materials and methods

Subjects

Twelve right-handed participants (eight female and four male; age range 19–30 years) with no neurological or psychiatric history and normal or corrected-to-normal vision participated in the study. All gave informed consent and the study conformed with the Code of Ethics of the World Medical Associations (Declaration of Helsinki). The project was approved by the relevant local Ethics Committee.

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Stimuli and task

The stimuli consisted of two spherical plastic objects (large object, 6 cm diameter; small object, 3 cm diameter; see Fig. 1A). The large object would normally be grasped with a WHG (between the thumb, the surface of the palm and all other fingers). The small object would normally be grasped with a PG (between the index finger and thumb). Although not instructed, all subjects adopted a WHG for the large object and a PG for the small object. A preliminary kinematic study ascertained that the chosen stimuli elicited distinct kinematic patterns for the small and the large stimuli. As classically found in a large number of reach-to-grasp studies (for review see Castiello, 2005), for the reaching component we found a longer movement duration (990 vs. 850 ms; $F_{1,11} = 43.21$, $P < 0.0001$), a prolonged percentage of arm deceleration time (68 vs. 64%; $F_{1,11} = 28.36$, $P < 0.0001$) and a lower arm peak velocity amplitude (470 vs. 589 mm/s; $F_{1,11} = 37.89$, $P < 0.0001$) for the smaller than for the larger stimulus. For the grasp component we found an anticipated (441 vs. 483 ms; $F_{1,11} = 61.54$, $P < 0.0001$) and lower (88 vs. 107 mm; $F_{1,11} = 78.64$, $P < 0.0001$) amplitude of maximum grip aperture for the smaller than for the larger stimulus. For the sake of clarity, we will refer throughout to the type of object-related distal motor acts as PG and WHG.

The objects were attached to the two sides of a rotating table, mounted on a plexiglass structure placed over the participant's body, and fixed to the sides of the scanner's patient bed (see Fig. 1B). Subjects were requested to perform two tasks: a grasping task, in which they were asked to reach towards and grasp the object naturally, and a reaching task in which they were asked to perform a movement towards the stimulus and touch it, maintaining the hand in a closed fist (the fist posture was the same for both small and large objects). The fist's posture was chosen so as to minimize distal involvement. The experimenter stood beside the scanner during the experiment to check whether participants performed proper grasping and reaching actions and to ensure that participants fixated the target object during both the reaching and the grasping actions. Trials in which the participants did not grasp the object appropriately or did not fixate the target were registered on a notation sheet and were not included in the analysis. The proportion of trials excluded from the analysis was 5%. Subjects were informed as to which task to perform by an auditory cue delivered through headphones (low pitch, grasping; high pitch, reaching). The sound also had a go-signal function in the sense that participants were allowed to start their actions toward the object only after a sound was delivered.

Experimental procedure

The experiment was conducted in an illuminated room so that the stimuli could be properly seen. Participants lay supine in the scanner with the head tilted forward ($\sim 30°$) and supported with a foam wedge, so as to enable them to see the stimuli. The stimuli were presented at the entrance of the scanner bore (above the pelvis) to permit comfortable reaching and grasping with the right hand. A point worth mentioning with respect to gaze direction is that, in contrast to classic neurophysiological and psychophysical reach-to-grasp studies, gaze direction was downward (see Fig. 1C). However, as revealed by our preliminary kinematic study, this constraint did not produce

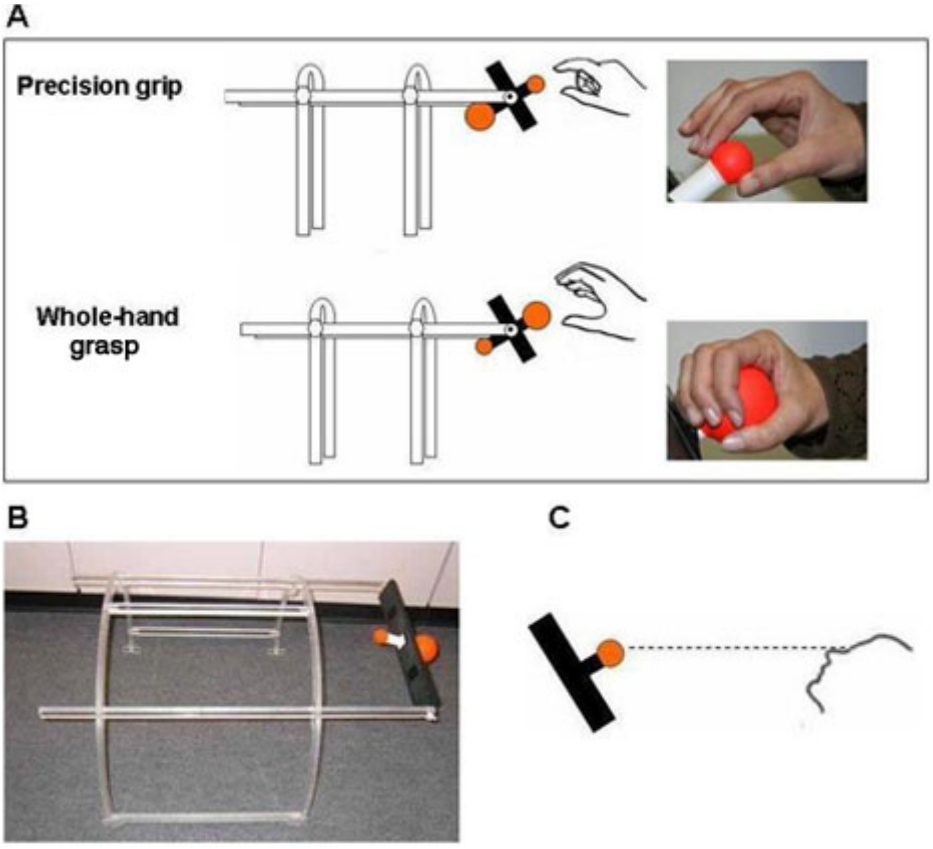

FIG. 1. Experimental apparatus. (A) Graphical representation of the two objects, the type of adopted grasp and the supporting structure. (B) Photograph of the apparatus. (C) Graphical representation of the subjects' gaze direction during the experiment.

changes in the classic kinematic patterning previously revealed for the two types of grasp under investigation. Furthermore, all previous studies which have attempted to investigate the neural correlates of grasping with fMRI have used similar procedures (e.g. Culham *et al*., 2003; Frey *et al*., 2005). In order to reduce head motion, the upper part of the arm was held close to the body with a strap above the elbow. The upper arm was also supported with a pillow. Between trials, participants were requested to keep their right hand in a relaxed position on the plastic plate of a belt they were wearing at the waist. This was done in order to maintain a constant hand starting position across trials and participants. Before the patient bed entered the magnet, the distance between the participant's hand rest position and the grasp target was adjusted such that the stimuli could be easily reached and grasped without any shoulder movement. Between trials, the experimenter manually switched the rotating table to determine the stimulus (small or large) for each trial, following a predetermined stimulus presentation sequence. The experimenter's hand (and body) were not visible to the participant while they performed this action.

Experimental design

An event-related design was used, with stimulus onset asynchrony (SOA) varying from 3 to 10 s, determined by a 'long exponential' probability distribution (Hagberg *et al*., 2001). Action toward the object (reaching or grasping) and object dimension (small or large) were manipulated as within-subjects variables, creating four different conditions: grasping small (GS), grasping large (GL), reaching small (RS) and reaching large (RL). Ninety trials per condition were administered in a semirandom order. Subjects switched from grasping to reaching trials (and vice versa) every five trials with stimulus dimension varying within each five-trial sequence. Action type (reaching or grasping) was grouped in sequences of five trials each, in order to minimize switching-related activations due to frequent changes from reaching to grasping and vice versa. Stimulus dimension (small or large) was fully randomized across trials, and varied within each five-trial sequence. The whole experimental session consisted of 360 trials per subject (90 trials for each of the four conditions), divided into eight runs of 45 trials each. SOA presentation was randomised independently for each run and each subject.

fMRI data acquisition

MRI data were acquired with a 3T scanner (Siemens Magnetom Trio) equipped with a standard Siemens birdcage headcoil. Functional images were acquired with a gradient-echo, echo-planar (EPI) T2*-weighted sequence in order to measure blood oxygenation level-dependent (BOLD) contrast throughout the whole brain [42 contiguous axial slices acquired with an interleaved sequence, 3 mm isotropic voxels, in-plane resolution of 64 × 64 voxels, field of view 192 × 192 mm, flip angle 90°, echo time (TE) 30 ms, bandwidth 2604 Hz/pixel]. Volumes were acquired continuously with a repetition time (TR) of 3 s; 89 volumes were collected in each single scanning run (4.27 min; eight scanning runs in total). High-resolution T1-weighted 3-D anatomical images were also obtained for each participant (MP-RAGE, 176 axial slices, in-plane resolution 256 × 256, 1 mm isotropic voxels, TR 1830 ms, TE 4.43 ms, flip angle 11°, bandwidth 130 Hz/pixel).

fMRI data analysis

Spatial preprocessing and analysis of the data were conducted using SPM2. For each subject the first four scans of each session were excluded from data analysis because of the nonequilibrium state of magnetization. For each participant, head movement was estimated and each volume was realigned to the first volume in the series and unwarped. To minimize the effect of artifactual motion-induced activations, regressors derived from the motion parameters were subsequently included in the model as nuisance variables. EPI images were normalized using the MNI152 template, supplied by the Montreal Neurological Institute and distributed with SPM2, and finally smoothed using a 6-mm full-width half-maximum Gaussian kernel. Functional data were also high-pass filtered (cut-off period 128 s).

Statistical analyses

As a first-level analysis, a General Linear Model (Friston *et al*., 1995) was computed for each subject, by modelling separately trials for the four event types (RS, Gs, RL, GL) and convolving these regressors with a canonical haemodynamic response function and its first temporal derivative (Friston *et al*., 1995). Trials were modelled as events of 2 s duration, starting at the onset of the sound which signalled that a movement should be made. Errors (incorrect actions) were modelled as separate events. For each subject, contrast images for each condition were created. These images were then entered into a second-level (random-effects) analysis in order to allow inferences across subjects that generalize to the population. A one-way ANOVA was conducted on the contrast images imported from the first level analysis (RS, RL, GS and GL), and paired *t*-tests were performed to compare grasping with the related reaching condition (Gs > RS; GL > RL). The resulting statistical parametric maps were thresholded at a family-wise error (FWE)-corrected *P*-value of 0.05 (voxel level).

To test our predictions concerning aIPS involvement in our tasks, a small-volume correction (SVC) was applied to this region of the left hemisphere. When the hypotheses clearly focus on a particular area, correction for multiple comparisons across the whole brain can be too conservative, and an SVC procedure can be more appropriate. The searching area was defined by reference to the confidence interval described by Frey *et al*. (2005) on the basis of many studies examining brain activity during grasping tasks. A 10-mm-radius sphere was built around the middle point of this interval (Talairach coordinates −38, −40, 41). Furthermore, *t*-maps resulting from these two contrasts (PG > reaching and WHG > reaching) were entered into a paired *t*-test in order to directly assess the grasping-related component of the activation.

The same SVC was also applied on the left ventral premotor cortex (vPMC), defininig the searching area on the coordinates suggested by Grèzes *et al*. (2003): −50, 5, 24, Talairach reference system. This was done because, in macaques, sensorimotor transformations of an object's intrinsic properties (e.g. size) into motor plans for configuring hand shaping are accomplished in a circuit connecting AIP with the inferior frontal cortex (area F5ab). We anticipated that the SVC applied to the left vPMC would not give any significant results (at the threshold used) for either PG or WHG.

Clusters were reported only if they survived a threshold of $P < 0.05$, FWE-corrected.

Localization

Locations of significant activations were expressed in Talairach coordinates (Talairach & Tournoux, 1988) converted from MNI space using the nonlinear transformation procedure developed by Matthew Brett (mni2tal, available at http://www.mrc-cbu.cam.ac.uk/Imaging/

Common/mnispace.shtml). To localize our activations with respect to previous 'grasping' studies (e.g. Frey *et al*., 2005) we referred to the Talairach Daemon database (Lancaster *et al*., 1997) implemented in the brain atlas developed by the Neurology University Hospital of Muenster (http://www.neuro03.uni-muenster.de/ger/t2tconv/index.html).

Results

As in previous work (Culham *et al*., 2003; Culham, 2004; Frey *et al*., 2005), activations related to PG and WHG were isolated by contrasting results from the grasp and reaching-only conditions.

Regions activated by the PG task

At the first-level analysis, comparison of the PG vs. reaching task identified for all participants significant sites of activation in the hemisphere contralateral to the performing right hand, corresponding to post- and precentral gyri (PostCG and PreCG, respectively). In addition, evidence of activation was also observed in the left intraparietal region, corresponding to Brodmann area (BA) 40 (Figs 2 and 3A). Paired *t*-tests, comparing the two grasping conditions with their related reaching movement (PG vs. RS and WHG vs. RL) were conducted. A second-level random-effects analysis was conducted, revealing activations in the left PostCG and PreCG, respectively (Fig. 3B and C and Table 1) and the cerebellum (Table 1). Activation clusters at similar stereotaxic coordinates have been reported in previous grasping imaging studies (e.g. Ehrsson *et al*., 2000; Culham *et al*., 2003).

Given our precise *a priori* anatomical hypothesis which was focused on the aIPS, a portion of the parietal cortex was adopted as a searching area for an SVC. This area was identified on the basis of the stereotaxic coordinates proposed by Frey *et al*. (2005) to circumscribe the 'grasping-dedicated' area in humans. This procedure revealed two further foci of activation within this area (Table 1), located in the inferior parietal lobe and corresponding to BA 40. Furthermore, SVC was also conducted on the right aIPS, referring to the stereotaxic coordinates suggested by Frey *et al*. (2005) for the right hemisphere (42, −38, 44). This procedure did not reveal any significant activations at the adopted threshold (FWE-corrected *P*-value of 0.05).

A similar result in terms of left contralateral aIPS activation exclusively for PG movements emerged when PG and WHG were directly compared (Fig. 4 and Table 1) and an SVC was applied (see Table 1).

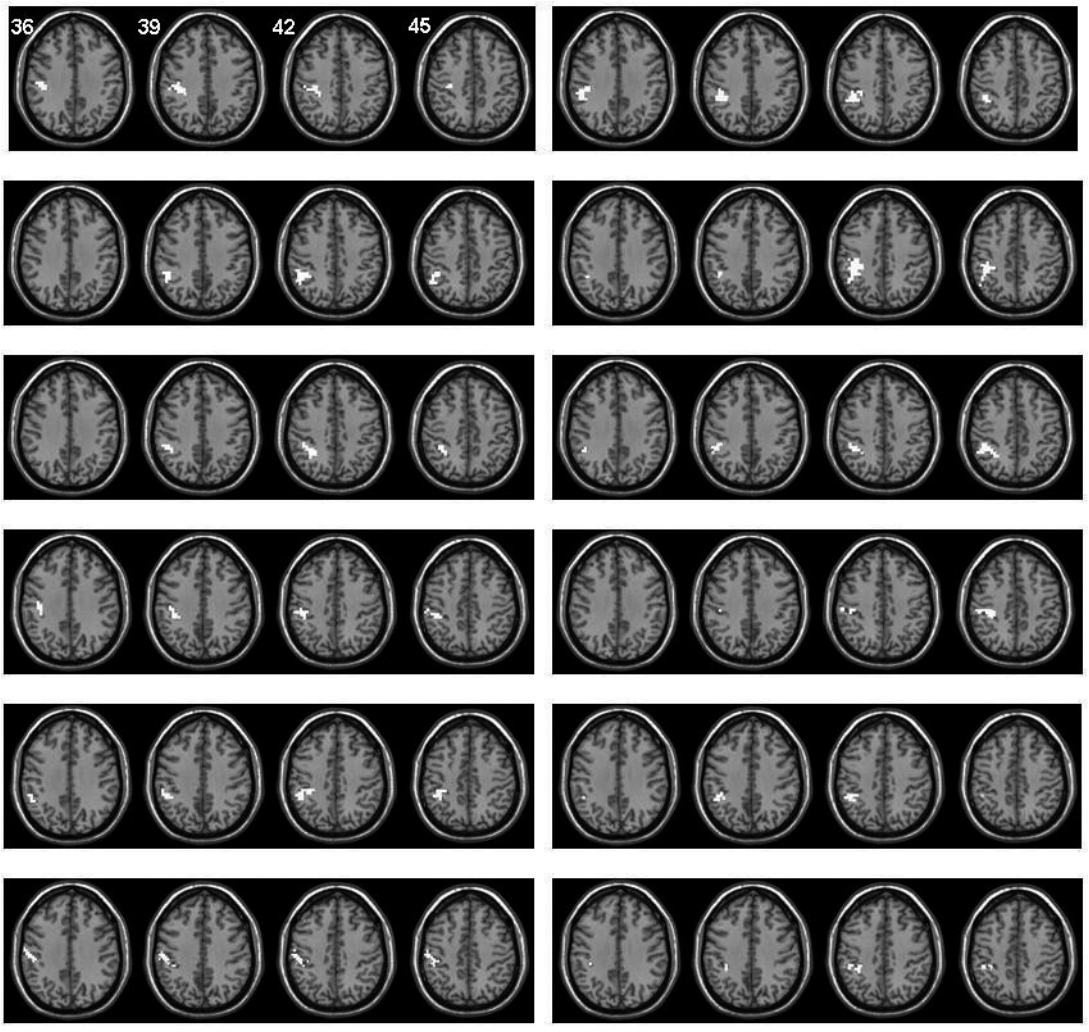

FIG. 2. Localization of grasp-related activity in the anterior parietal region of interest only for PG movements in the 12 participants. Single-subjects normalized functional data are projected on the template provided by the software MRIcro.

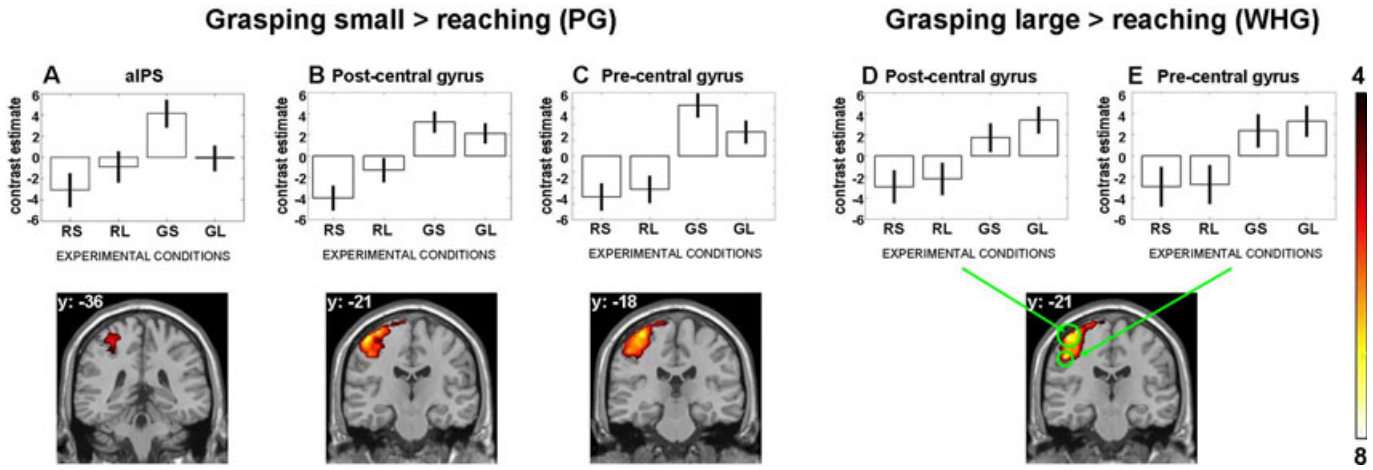

FIG. 3. Localization of grasping-related cortical activity. Statistical parametric maps (*t*-statistics) of activations resulting from the random-effects analysis contrasting the reach-to-grasp with the reaching-only conditions ($P < 0.05$, FWE-corrected for multiple comparisons). For the precision-grip task, activations were observed (A) within the intraparietal region, as well as (B and C) within the left post- and pre-central gyrus while (D and E), for the WHG, significant activations were detected only within the post- and pre-central gyrus. Histograms represent the contrast estimates for the activated areas for the four experimental conditions.

TABLE 1. Activations associated with the grasp tasks

		Cluster level	Voxel level					
Area	BA	*P*-value	*k*	*P*-value	*t*-value	*x*	*y*	*z*
PG > Reaching								
L Pre-central gyrus	4	0.000	160	0.000	7.59	−33	−18	48
L Post-central gyrus	3			0.001	7.12	−48	−21	45
L Inferior parietal lobule†	40	0.003	11	0.017	4.19	−33	−36	48
L Inferior parietal lobule†	40			0.028	4.00	−33	−33	43
R Cerebellum, culmen		0.000	122	0.000	8.03	21	−51	−20
R Cerebellum, culmen				0.012	6.29	15	−50	−13
WHG > Reaching								
L Post-central gyrus	3	0.000	168	0.021	5.92	−42	−21	57
L Pre-central gyrus	4			0.032	4.94	−48	−15	39
R Cerebellum, culmen		0.000	20	0.002	5.90	21	−48	−18
PG > WHG								
L Inferior parietal lobule	40	0.000	13	0.003	6.32	−36	−45	38

BA, Brodmann area; *k*, number of activated voxels; L, left; R, right. All the coordinates are in Talairach space. *P*-values corrected (FWE) for multiple comparisons ($P = 0.05$). †Values obtained with the small-volume correction.

Regions activated by the whole-hand task

The comparison WHG vs. reaching did not reveal any aIPS activation. However, as for the PG task, activity within the contralateral Post- and Pre-CG was found (see Fig. 3D and E, respectively; Table 1). Activations within the Post-CG (primary sensorimotor area, BA 3) were more dorsally located with respect to activations detected in the same area for the PG task. Similarly, activations detected within the Pre-CG (primary motor cortex, corresponding to BA 4) involved a more dorsal region with respect to the Pre-CG activation revealed for the PG task. Finally, for the WHG task right cerebellar activations (culmen) were observed (Table 1). Importantly, when contrasting WHG with PG no differential activity was observed. In order to reveal activity in aIPS in this contrast the threshold had to be lowered to $P < 0.001$, uncorrected.

Discussion

The crucial aspect of our fMRI results is the finding that, in humans, the aIPS seems to be involved in PG but not in WHG at the adopted statistical threshold. This may suggest that there may be a small portion of aIPS where WHG is encoded and a larger portion where PG is encoded.

Selective contribution of aIPS to PG movement

Several prior studies using similar methods to ours have reported activation in aIPS for grasping actions. Although these studies manipulated the size and shape of the objects, participants were required to use only a PG regardless of the object's size and shape (Binkofski *et al*., 1998; Culham *et al*., 2003, 2004; Frey *et al*., 2005). Therefore whether aIPS has a special role in grasp type was essentially unknown.

Our findings resolve this issue by showing that significant activity in aIPS (at the adopted significance threshold) was confined to the PG task. Related, converging evidence comes from an inactivation study in macaques (Gallese *et al*., 1994). Transient inactivation of AIP, by injecting a GABA-receptor agonist (muscimol) into the rostral IPS posterior bank, produced a change in the

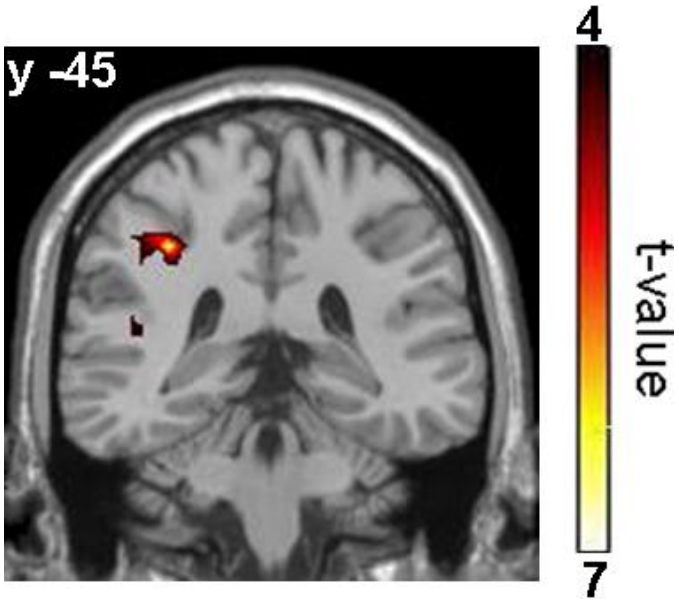

FIG. 4. Statistical parametric map (*t*-statistic) of activations resulting from the random-effects analysis contrasting PG with WHG ($P < 0.05$, FWE-corrected for multiple comparisons). Significant activations were observed only within the left aIPS.

performance of visually guided movements during grasping tasks. Grasping errors were observed only in difficult tasks that required a PG to grasp a small cube or a small sphere (as in the present experiment). Therefore the difference in activation between PG and WHG may reflect the need for additional sensory–motor control mechanisms for PG. In humans, evidence from developmental, psychophysical and neuropsychological studies seems to suggest that PG is characterized by a greater degree of complexity. Firstly, the ability to perform independent finger movements and grasp with the PG is not present when voluntary grasping emerges (e.g. Gordon, 1994). Secondly, consistent results within the adult reach-to-grasp behavioural literature (for review see Castiello, 2005) indicate that the performance of a PG is characterized by the need for additional time. This allows the use of feedback in order to meet the more precise requirements for grasping a small object and allows for the independent use of the index finger and thumb. Thirdly, following lesions involving aIPS, the ability to perform a WHG remains unaltered whereas the ability to perform a PG movement is lost and rarely recovers (Jeannerod, 1986). Finally, aIPS may be activated for the control of fine PG forces in the range typically used for the manipulation of small objects (Ehrsson *et al*., 2000, 2001). In this respect, we naturally use PG when objects are apparently light or fragile, as deduced by their size or by the internal model we have of the object. Thus, activation of the aIPS may be primarily triggered by the apparent- or known weight of the object rather than by the type of grasp used. Although this might be a possibility the fact that we also found activity in the IPS for WHG (though at a lower threshold) might favour the 'type of grasp' hypothesis.

M1 and cerebellar contribution to PG and WHG

In contrast to the PG selective activation found in aIPS, M1 was active in a similar manner for both PG and WHG tasks. This could be explained on the basis of the different roles played by these brain centres in motor control. Whereas electrophysiology in primates (Rizzolatti & Luppino, 2001) and brain imaging studies in humans (Ehrsson *et al*., 2000; Grèzes *et al*., 2003) show that, respectively, AIP and aIPS activity mainly relates to goal-directed actions, activity within M1 appears to be more related to movements, independently of the action goal. Moreover, reversible inactivation studies performed on aIPS (Gallese *et al*., 1994) and M1 (Fogassi *et al*., 2001) show that, while inactivation of area M1 leads to a global impairment of grasping behaviour, inactivation of AIP mainly affects PG and particularly the visuomotor transformation of the to-be-grasped objects.

The present results also provide further evidence that the cerebellum is necessary for the adaptive adjustment of motor output and sensorimotor coordination. As demonstrated by Mason *et al*. (2006), these mechanisms could have great utility for adjusting hand shape during reach-to-grasp. Furthermore, recent neuroanatomical studies confirming cerebellar projections to M1 and AIP (Clower *et al*., 2005) add an additional layer of complexity to the process involved in the transformation of the visual properties of a 3-D object into the appropriate hand movement to manipulate that object. Our findings of cerebellar activity together with aIPS and M1 activity for different types of grasp seem to support this view.

The lack of premotor activity

One remaining question concerns our failure to detect significant activation in vPMC and/or inferior frontal cortex, respectively. In macaques, it has been revealed that AIP may furnish area F5 with visual signals of objects to aid in the selection of appropriate grasp configurations. The AIP–F5 network can then use the physical object properties to select the suitable motor schema according to the goal of the action (Rizzolatti & Luppino, 2001). Of relevance is that, of the F5 neurons active during grasping, the most frequent were those involved in PG (Rizzolatti *et al*., 1988) whereas WHG neurons were encountered much less frequently (Rizzolatti *et al*., 1988; Jeannerod *et al*., 1995). Therefore, if we had revealed vPMC activations it could have been argued that the higher level of activity in the human aIPS for PG movements could be an indication that neural activity is also correlated with specific goal-related distal motor acts in this area, and that the specific aIPS activations for PG arise from its reciprocal connections with vPMC (Luppino *et al*., 2004). However, we found no evidence of significant premotor activations (remember that the SVC applied to the left vPMC did not give any significant results for either PG or WHG). Detection of activity in this region during visually guided grasping has been inconsistent, with some studies reporting effects (Ehrsson *et al*., 2000) and others not (Culham *et al*., 2003; Frey *et al*., 2005). Furthermore, Binkofski *et al*. (1999) and Ehrsson *et al*. (2000) identified responses in premotor cortices with haptic manipulation and isometric grasping tasks, respectively, not in visually guided grasping. The reasons for these differences remain unclear. One possibility is that the inferior frontal activations might be recruited for any goal-orientated task, whereas aIPS might be specific to those involving hand affordance (Iacoboni *et al*., 1999; Frey *et al*., 2005). As such, both the reaching and the grasp task used in the present experiment required specific motor goals. Consequently, activations within inferior frontal areas could have cancelled one another out when compared. Support for this hypothesis comes from *post hoc* analyses in which we compared reaching and grasping tasks. We found inferior frontal activations

TABLE 2. Activations within inferior frontal areas for both the reaching and the grasping task performed towards the small and the large objects

		Cluster level	Voxel level					
Area	BA	*P*-value	*k*	*P*-value	*t*-value	*x*	*y*	*z*
Reaching small								
L Inferior frontal gyrus	44	0.000	42	0.000	6.93	−53	10	15
Reaching large								
L Inferior frontal gyrus	44	0.000	27	0.000	6.15	−45	16	10
Grasping small								
L Inferior frontal gyrus	44	0.000	44	0.000	7.71	−50	4	6
Grasping large								
L Precentral gyrus	6	0.000	25	0.000	6.86	−55	3	16

BA, Brodmann area; L, left; *k*, number of activated voxels. All the coordinates are in Talairach space. *P*-values corrected (FWE) for multiple comparisons ($P = 0.05$).

for both reaching and grasping performed towards the small and the large objects (see Table 2).

Conclusions

The present findings have significantly extended our understanding of the neural bases of visually guided grasping. In line with current literature on the neuroimaging of grasping, we found evidence that aIPS is involved in the execution of grasping. However, we broaden this literature demonstrating that aIPS involvement varies depending on the type of grasp performed. We observed a reliable aIPS activation only during the performance of PG tasks, whereas activation for WHG tasks was absent at the adopted significance threshold.

This study opens several interesting directions to pursue. First, our findings of left parietal activation may reflect a contralateral organization given that only the right hand was used in these tasks. This fits well with previous observations demonstrating contralateral aIPS activation in a grasping task (e.g. Frey *et al*., 2005). However, neuroimaging results are equivocal in this respect and activations confined to the right hemisphere (Ehrsson *et al*., 2000) and bilateral activations (e.g. Binkofski *et al*., 1998; Culham *et al*., 2003) have also been found for visually guided grasping. Further work in which both arms are investigated is needed to evaluate the specific task demands related to differences in the laterality of aIPS activity.

Second, current views on aIPS suggest that aIPS is not a simple repository for grasp configurations but performs iterative comparisons during an ongoing movement between an efference copy of the motor command and incoming sensory information, in order to ensure that the current grasp plan matches the current context and sensorimotor state (Tunik *et al*., 2005; Rice *et al*., 2006). In this connection it has been proposed that aIPS is critical for error detection during visually guided reach-to-grasp movements (Tunik *et al*., 2005). So far, this hypothesis has been tested in experiments which have primarily used PG grasping tasks (Tunik *et al*., 2005; Rice *et al*., 2006). Therefore, the aIPS function of dynamic control should be further tested by looking at a broader range of motor representations that lead to the coupling between object size and hand configurations.

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Abbreviations

AIP, anterior intraparietal sulcus; aIPS, anterior intraparietal sulcus; BA, Brodmann area; fMRI, functional magnetic resonance imaging; FWE, family-wise error; GL, grasping large; GS, grasping small; PG, precision grip; PostCG, postcentral gyrus; PreCG, precentral gyrus; RL, reaching large; RS, reaching small; SVC, small-volume correction; vPMC, ventral premotor cortex; WHG, whole-hand grasp.

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