Research report

Cortical topography of human anterior intraparietal cortex active during visually guided grasping

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Abstract

Dexterous manual prehension requires successfully transforming sensory representations of an object's intrinsic spatial properties (e.g., shape) into motor plans for configuring the opposition space of the hand. In macaques, these sensorimotor transformations are accomplished in a circuit connecting the anterior intraparietal sulcus (area AIP) with inferior frontal cortex (area F5ab). Activation in the human anterior intraparietal sulcus (aIPS) during visually guided grasping suggests a homologue of macaque area AIP. If true, then despite individual variation in cortical topography, visually guided grasping should be consistently associated with focal activation at the junction of the IPS and postcentral sulcus. FMRI was used to test this hypothesis in 14 right-handed adults.

Despite substantial variability in IPS topography, a contrast between pincer grasping vs. reaching to complex asymmetrical shapes revealed activation foci at the junction of the IPS and postcentral gyrus in all 14 individuals. This site is likely within the most superior, rostral aspect of Brodmann's area 40, corresponding to area PF or PDE as defined by von Economo and Koskinas, and area 86 as defined by Vogt and colleagues. In both humans and macaques this region appears to play a key role in visually guided grasping.
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1. Introduction

Effective grasping involves transforming representations of objects' intrinsic spatial properties (e.g., shape) into motor programs for configuring the hand [20,21]. In *Macaca*, these sensorimotor transformations are accomplished in a circuit connecting the anterior-most region within the lateral bank of the intraparietal sulcus (area AIP) with area F5ab [32,34].

Area AIP was first identified as separate from more posterior lateral (LIP) and ventral (VIP) intraparietal areas by Preuss et al. [31]. In macaques, inferior parietal lobule area 7b extends into the IPS, "covering the outer one-third to one-half of the lateral bank (p. 483)." Area AIP includes the deepest part of the anterior lateral bank and fundus and consists of a "single zone of thin cortex (p. 484)." While LIP and VIP are connected with visual cortex, area AIP is connected with sensorimotor cortex.

Electrophysiological recordings in macaques identified cells in the lateral bank of the IPS that are involved in the visual guidance of object-oriented hand movements [38]. These cells vary in the extent to which they are selective for specific objects. Of greatest relevance to visually guided grasping are those cells that demonstrate a high degree of object selectivity, while nonselective cells may be responding to proximal movements common to a variety of object manipulation tasks ([35, p. 431]). These highly selective

cells can be classified into several groups depending on their receptive field (RF) properties. Motor dominant neurons require no visual input and therefore discharge in either the light or dark during manipulation. These cells do not respond to object fixation and may therefore be coding hand movements necessary to engage objects. Visual–motor neurons respond more strongly to object manipulation in light but also respond when neither the hand nor target object are visible. In addition, the object type of visuomotor neurons respond when the preferred object is fixated in the absence of manipulation, suggesting that these cells are coding hand movements relative to objects' visual properties. Finally, visual neurons only respond when an object is manipulated in the light, or when it is fixated. These cells are likely coding visual properties of objects that are useful for manipulation [35,36].

Object-selective cells within these three classes are distributed in a gradient along the lateral bank of the IPS. Visual dominant cells are found in higher concentrations in area LIP. Movement-related motor and visual–motor dominant units are also found in LIP but are more concentrated immediately posterior to the hand representation in primary somatosensory cortex (SI), in area AIP [35]. The specific role of these units in grasping is confirmed by the fact that injections of a GABA agonist (muscimol) into area AIP cause a reversible deficit in preshaping the hand when grasping visual objects [12] while leaving reaching unaffected.

In sum, both anatomical and electrophysiological evidence suggest that an area located in the lateral bank of the IPS at the junction with the postcentral sulcus is involved in the control of visually guided manipulation of objects in macaques. An important issue concerns whether a homologous system exists in the human brain.

1.1. Evidence for a human homologue of AIP

As summarized in Table 1, recent fMRI studies identify activity within the anterior portion of the IPS (aIPS) in tasks that evoke responses in cells of macaque AIP. Like motor dominant neurons, manipulation of complex vs. simple shapes without vision is associated with mean activation in the rostral portion of BA40 in humans [2]. This location is also activated during haptic recognition of shapes [19]. Consistent with visual–motor units, activation within this vicinity is also observed during object discrimination tasks involving both visual-to-tactile and tactile-to-visual transfer [17]. Activity associated with grasping visually presented 3-D objects [1], or grasping at 2-D projected objects [6], is centered within a slightly more lateral and anterior site. Like visually dominant manipulation cells, viewing manipulable tools is associated with activation in anterior BA40 [5]. Activity in aIPS has also been reported during visual discrimination of objects' surface orientations [37].

There is considerable interindividual variation in the cortical topography of the IPS. Consequently, a strong test of a hypothesized homologue of macaque AIP in the human brain necessitates analysis at the level of the individual. Binkofski et al. [1] provides such data for four individuals in a task that involved grasping 3-D symmetrical shapes. Here we explore whether visually guided grasping of more complex shapes is associated consistently with focal activation at the junction of the IPS and postcentral sulcus in a larger sample of 14 individuals.

1.2. Computing hand opposition space

An essential component of visually guided grasping is configuring the hand so that opposing forces applied by the

Table 1
Standardized coordinates of anterior intraparietal activations associated with several different functional neuroimaging tasks

	Task	X	Y	Z
A				
Binkofski et al. [2]	Haptic manipulation	−40	−40	40
Binkofski et al. [3]	Haptic manipulation	−48	−34	40
Culham et al. [6]	Visually guided grasping			
Chao and Martin [5]	Viewing graspable tools	−32	−47	42
Chao and Martin [5]	Naming graspable objects	−30	−39	47
Culham et al. [6]	Visually guided grasping	−38	−48	52
Grefkes et al. [17]	Cross-modal transfer	−40	−42	36
Jancke et al. [19]	Manual exploration	−44	−40	40
Shikata et al. [37]	Visual discrimination of surface orientation	−37	−40	47
Summary	95% Confidence Interval:	(−34, −42)	(−37, −43)	(38, 44)
B				
Binkofski et al. [2]	Haptic manipulation	40	−40	44
Binkofski et al. [3]	Haptic manipulation	48	−34	40
Culham et al. [6]	Visually guided grasping	40	−50	50
Jancke et al. [19]	Manual exploration	36	−44	44
Shikata et al. [37]	Visual discrimination of surface orientation	45	−32	51
Summary	95% Confidence interval	(37, 47)	(−33, −42)	(40, 48)

The upper panel lists areas within the left hemisphere, and the lower panel lists those detected in the right hemisphere. All coordinates are in the reference frame of Talairach and Tournoux [39].

digits cancel through an object's center of mass (COM) [4]. In the case of a pincer grasp this is accomplished by positioning the fingers on opposable surfaces such that the opposition vector connecting these two points passes through the COM [27, pp. 81–83]. For simple objects with compound symmetry (e.g., spheres, squares, and rectangles) this problem is relatively easy to solve. By contrast, it becomes more computationally demanding for asymmetrical objects with complex surface geometries [4]. Nevertheless, even when confronted with complex, asymmetrical shapes occurring in a variety of orientations, human actors rapidly configure their grip such that the opposition vector passes through, or very close to, the COM [14]. On the basis of available evidence it is tenable that AIP and its putative homologue in the human brain may play a critical role in this behavior.

2. Experiment 1: effects of shape, orientation and location on opposition vector selection

Measuring the relationship between the opposition vector and an object's COM provides a means of quantifying the accuracy with which an object is grasped. Quantifying opposition vectors during fMRI testing was not technically feasible. Yet, it was essential to determine subjects' accuracy when performing this task with the same apparatus and stimuli used in the neuroimaging study. In addition, it was necessary to demonstrate that subjects choose opposition vectors accurately when grasping stimuli fixed in the vertical plane and located at different positions along the horizontal axis. This is a potentially important difference from earlier psychophysical investigations, and one that is necessitated by the constraints of the MRI testing environment of the subsequent main experiment. Without these results we would be uncertain whether this task was accomplished in the scanner similarly to the way it is accomplished in standard psychophysical testing. Therefore, we undertook a preliminary psychophysical investigation validating the stimuli and apparatus used in the main fMRI experiment detailed below. Stimulus objects were a subset of those shapes created by Blake et al. [4] and used in psychophysical testing in Ref. [14]. Similar to Goodale et al., we varied the orientations in which these shapes were presented. However, in the present study objects were presented in the vertical rather than the horizontal plane, and their spatial locations also varied along the horizontal axis. Given the flexibility of visually guided grasping in everyday environments, we reasoned that these factors should not influence the accuracy with which opposition points are selected.

2.1. Method

Eight healthy, right-handed adults (two females, six males, age 20–25 years) participated for course credit. At the beginning of the study, the pads of the right index finger and

thumb were brought together in a pincer grip. A pen was used to make two small ink lines indicating the centers of the tips of the thumb and forefinger.

2.2. Stimuli

As shown in Fig. 1A, shapes used in this study were based upon the templates used by Blake et al. [4] to develop algorithms for the control of grasping in two-fingered robots. These shapes lack clear symmetry and have smoothly bounded contours. Four of these shapes (column A) were selected randomly for use in our psychophysical testing.

As illustrated in Figs. 1B and 1C, the apparatus consisted of a 14.5 × 36.5 cm vertical, black, wooden platform inserted into a 21.5 × 56 cm horizontal wooden base. On the right side of the base was an 8 × 8 cm Plexiglas window. A minidigital camcorder was positioned on a tripod immediately below this window. Focal length of the camera to objects placed on the Plexiglas surface was adjusted to 2× and remained constant throughout the experiment. Four
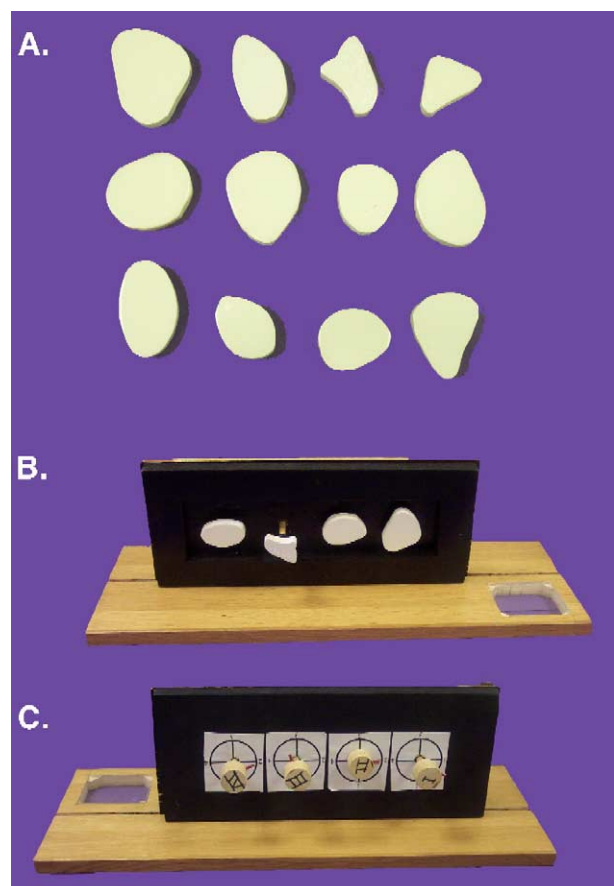

Fig. 1. Apparatus and stimuli used in Experiments 1 and 2. (A) Set of 12 stimuli used in Experiments 1 (top row) and 2 (all rows). (B) View of the apparatus from the subjects' perspective with one stimulus advanced. (C) View of the rear of the apparatus showing how the orientation of stimuli is controlled by the experimenter.

5-mm diameter horizontal spindles (locations A, B, C, D) fit through holes in the vertical platform located 7 cm above the horizontal base and separated by 6 cm. Each spindle had a knob with a pointer on the end facing the experimenter. The ends of the spindles facing the subjects had small brass screws passing through them. Each stimulus object had a 5-mm diameter hole with a small notch cut in its backside. This allowed the stimuli to be attached to the ends of the spindles in only one orientation, with the objects' notches fitting over the brass screws. By turning the knobs, the experimenter could precisely rotate the objects to specific test orientations by aligning the pointers with angular degrees marked on the rear of the vertical platform (0°, 90°, 180°, and 270°). By pushing in a knob, the experimenter could advance a stimulus object by 3 cm toward the subject. Small rubber bumpers on the spindles ensured that objects would all be at the same distance from the subjects when retracted. The apparatus was positioned on a table such that its vertical plane was located 50 cm from the actor. When viewed from 50 cm stimulus objects subtended approximately 3–5° of visual angle measured along their principal axes. The starting position of the hand was 40 cm in front of the apparatus' vertical plane and aligned with its center. Vision was controlled with a pair of liquid crystal goggles (Translucent Technologies, Toronto) initiated by a microcomputer.

Trials began with vision occluded and the right-hand palm down on the starting position. A single stimulus object was placed on one of the four spindles, rotated into its test orientation, and advanced toward the subject. When the stimulus was in position, the subject was given a verbal "ready" signal and after approximately 500 ms the experimenter pressed a computer key that triggered the goggles to clear. Subjects were instructed to reach for and grasp the nearest object using their right thumb and forefinger and remove it from the spindle as quickly as possible. They then placed the object backside down on the Plexiglas window and held it there for approximately 2 s while the digital video camera captured the position of the thumb and forefinger on the object. The hand was then returned to the starting position, vision was occluded, and the next trial was prepared. Each stimulus shape (4) appeared in all positions (4) and orientations (4) a total of two times in counterbalanced order. Each subject was given eight practice trials.

2.3. Data analysis

Distance of the opposition axis from the COM was manually coded from digital video. Transparencies with tracings of the objects' shapes and COMs were created. For each trial, a frame displaying the backside of the stimulus being grasped by the thumb and forefinger was displayed on a video monitor and traced onto a corresponding object transparency. Distance between the opposition vector and the COM was then manually measured by overlaying a

second transparency consisting of a series of concentric rings spaced 2 mm apart. The center of this measurement transparency was aligned with the COM on the underlying object transparency. Because of the 2× scaling factor of the digital images, each ring represented 1 mm of actual distance. Distances of the opposition axes from the COM were manually entered into a spreadsheet. Mean distances were calculated separately for each subject and submitted to a repeated measures ANOVA with shape (4), orientation (4), and position (4) as fixed factors.

2.4. Results and discussion

Consistent with earlier findings [14], subjects reliably configured their grips such that opposition vectors passed through, or very near to, objects' COMs. This was true even though objects in the present study were presented in the vertical plane and at different positions along the horizontal axis. For all four shapes mean distances of the opposition axes from the COMs were equal to or less than 1.71 mm. Though small in absolute terms, the difference in accuracy between shapes was significant [$F(3,15) = 7.5$, $P = 0.003$, MSE = 0.95] reflecting the fact that some objects were more difficult than others. Consistent with earlier observations [14], stimulus orientation did not significantly affect performance, $F = 1.0$, $P = 0.40$. The same was true for stimulus position, $F < 1.0$. All two- and three-way interactions were nonsignificant, $P > 2.0$ in all cases.

In sum, results of this initial study are consistent with earlier work showing that when using pincer grips to engage complex, asymmetrical shapes, actors reliably choose opposition axes that pass through objects' COMs. This is true even when objects are presented at different orientations and positions in the vertical plane. These findings allowed us to use this paradigm to investigate the role of the human aIPS in visually guided grasping.

3. Experiment 2: role of putative aIPS in visually guided grasping

As noted earlier, Binkofski et al. [1] demonstrated activation in aIPS in four individuals when they grasped vs. pointed to 3-D rectangles. Given their bilateral symmetry, achieving a stable grasp with these objects is considerably less demanding than with the complex asymmetrical shapes used in Experiment 1. The latter task should place greater demands on sensorimotor transformations for grasping and therefore serve as a useful tool for mapping areas involved in these computations in a larger number of individual subjects. To the extent that the aIPS of humans is a crucial component in using visual shape to determine opposition space of the hands, we expected to observe activation in all 14 individuals at the junction of the IPS and postcentral sulcus when comparing reaching-to-grasp vs. reaching-to-point at the stimuli.

3.1. Method

Fourteen healthy adult subjects (five female, nine males; mean age = 24.4, range 20–45) provided informed consent in accordance with the Dartmouth Institutional Review Board. All were strongly right handed according to the Edinburgh Handedness Inventory [28].

Stimulus shapes consisted of all 12 objects used by Goodale et al. [14] and developed by Blake et al. ([4], Fig. 1A). Stimuli were presented using the apparatus described in Experiment 1. Because the liquid crystal goggles are not compatible with MRI, vision was controlled by instructing subjects when to open and close their eyes. Compliance was monitored by an experimenter located in the gantry. Timing of the conditions was controlled by the experimenter who received auditory cues through MR-compatible headphones. Timing of auditory cues was controlled by a microcomputer running Presentation software (http://nbs.neuro-bs.com).

Subjects reclined in a supine posture and the apparatus was secured around their waists with a Velcro strap such that the vertical plane was located at the entrance to the bore. Each subject performed six runs consisting of three epochs. Each epoch consisted of three blocked conditions presented in the following fixed order: point, grasp, and rest. Each condition lasted for 28 s with a 5-s interblock interval. At the beginning of each epoch the experimenter randomly selected four of the objects without replacement from a bin containing all 12 stimuli and placed them onto the spindles. A counterbalancing list was used to determine the order in which stimuli on the four spindles were presented. As in Experiment 1, the test stimulus for a given trial was cued by advancing it toward the subject.

Each block began with the subject lying motionless, eyes closed. The experimenter was given an auditory cue to tap the subject on the right thigh. For point and grasp conditions, this tap signaled the subject to open his/her eyes and begin the task. During the point condition, subjects used the right index finger to contact the center of the advanced stimulus object and push it back to the vertical plane. They then retracted their hand to the start position and waited for the experimenter to advance the next stimulus. During the grasp condition, the right thumb and index finger were used to pincer grip the object, remove it from the spindle, and drop it. In the rest condition, subjects remained motionless with their eyes closed after receiving the tap.

In both the point and grasp conditions, the experimenter received auditory cues to advance the stimuli every 7 s. After contacting the fourth object, the subject closed his/her eyes and waited for a tap signaling the start of the next condition. There was a 5-s break between each condition.

3.2. Magnetic resonance imaging

Imaging was performed with a General Electric Horizon whole body 1.5 T MRI scanner using a standard birdcage head coil. Head movements were minimized by use of a foam pillow and padding. Prior to each functional run, four images were acquired and discarded to allow for longitudinal magnetization to approach equilibrium. Within each functional run, an ultrafast echo planar gradient echo imaging sequence sensitive to blood oxygenation level-dependent (BOLD) contrast was used to acquire 25 slices per TR (4.5 mm thickness, 1 mm gap, in-plane resolution 3.125×3.125 mm). The following parameters were used: TR = 2500 ms, TE = 35 ms, flip angle = 90°. A high-resolution, T1-weighted, axial fast spin echo sequence was used to acquire 25 contiguous slices (4.5 mm slice thickness with 1.0 mm gap) coplanar to the BOLD images: TE = Min full, TR = 650 ms, echo train = 2, FOV = 24 cm. High resolution ($0.94 \times 0.94 \times 1.2$ mm), whole brain, T1-weighted structural images were also acquired using a standard GE SPGR 3-D sequence.

3.3. Image processing

Structural and functional images were preprocessed and analyzed using SPM99 (http://www.fil.ion.ucl.ac.uk/spm). Functional data for each individual subject were corrected for head motion. Functional and structural images were coregistered and transformed into a standardized, stereotaxic space (MNI template). This resulted in 25 axial slices of isotropic, 3.125 mm^3 voxels. Data were smoothed with an 8 mm FWHM, isotropic Gaussian kernel, and temporally filtered with a cutoff twice the epoch length (198 s).

First-level analyses were performed on individual subjects' data. Results of these analyses were also submitted to a second-level, random effects analysis, with subjects as the random variable [11]. For both fixed and random effects analyses, statistical activation maps were constructed on the basis of differences between trial types using a t statistic. Clusters consisting of at least five voxels, separated by a minimum of 8 mm and having t values equal to or greater than 2.57 ($P < 0.01$, uncorrected for multiple comparisons), were considered statistically significant for individuals. Population-based significance was corrected for multiple comparisons at a threshold of $P < 0.05$.

The resulting t map for each subject was rendered on their individual high resolution structural MRI using MRIcro software (http://www.psychology.nottingham.ac.uk/staff/cr1/mricro.html). This allowed us to "erode" the cortical surface to reveal activations within sulci, thus skirting errors associated with surface projection methods. Anatomical localization was made both by visual inspection and comparison with neuroanatomy atlases using 2-D and 3-D rendering [8], and by registering the MRI studies in a standard space based on the Talairach coordinate system [39]. Conversion into this standard space was accomplished by using a nonlinear algorithm (http://www.mrc-cbu.cam.ac.uk/Imaging/mnispace.html). Fig. 2 illustrates the locations
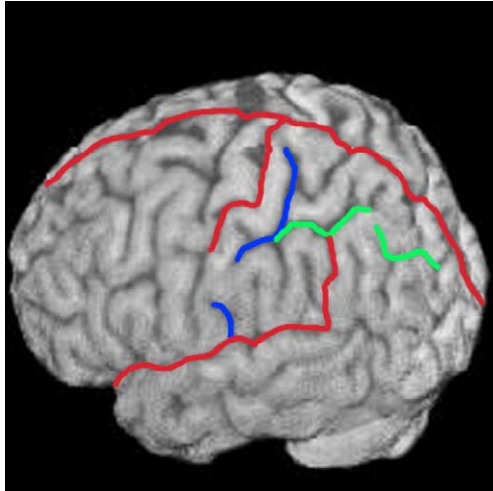
Fig. 2. Locations of major sulci illustrated on a 3-D rendering of an individual subjects' T1-weighted MRI scan. Locations of grasp-specific activations were confirmed on an individual basis by identifying locations of major parietal sulci: intraparietal sulcus (IPS, green) and the postcentral sulcus (blue). The central and lateral sulci and longitudinal fissure are colored red. Note that the postcentral and IPS sulci are interrupted in this individual. These are two commonly observed variants in parietal topography amongst individuals.

of major sulci in one individual localized using this method. Region-of-interest (ROI) analyses were performed using customized masks for each individual that excluded all data located outside the left parietal lobe.

4. Results

All subjects were able to complete the point and grasp tasks without errors. As has been done previously, activations related to pincer grasping were isolated by contrasting results from the grasp and point conditions [1,16].

4.1. Random effects group comparison

Comparison of the grasp versus pointing task identified two significant sites of activation in the hemisphere contralateral to the performing right hand. As illustrated in Fig. 3A, the first area is located in the left parietal cortex at the approximate intersection of the IPS with the postcentral sulcus (Talairach coordinates: −40, −33, 43; peak $t(13)$ = 8.48). This site is likely within the most superior, rostral aspect of BA40, corresponding to area PF or PDE as defined by von Economo and Koskinas [40], and area 86 as defined by Vogt and colleagues [41]. Fig. 3B shows that the second activation is located in the left lateral sulcus extending into the parietal operculum (SII; standardized coordinates: −51, −22, 10; peak $t(13)$ = 8.38).

4.2. First-level individual analyses

Given our a priori hypothesis, results of individual subjects' t maps were masked to only show activations in the left parietal lobe ROI using the procedure detailed above. As illustrated in Fig. 4, despite significant variability in cortical
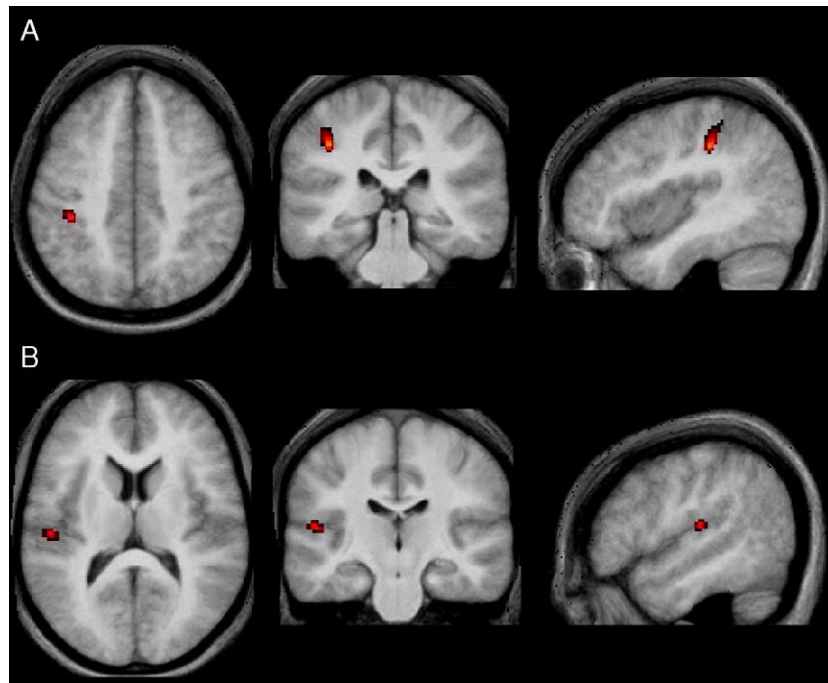

Fig. 3. Localization of grasp-specific cortical activity in left parietal lobe. Statistical parametric maps (t statistic) of activations resulting from the random effects analysis contrasting reach-to-grasp vs. reach-to-point conditions ($P < 0.05$, corrected for multiple comparisons) superimposed on the mean of 14 subjects' T1-weighted anatomical scans. (A) Significant activation is observed within the left aIPS and (B) a site spanning the lateral fissure that includes parietal operculum (putative SII).
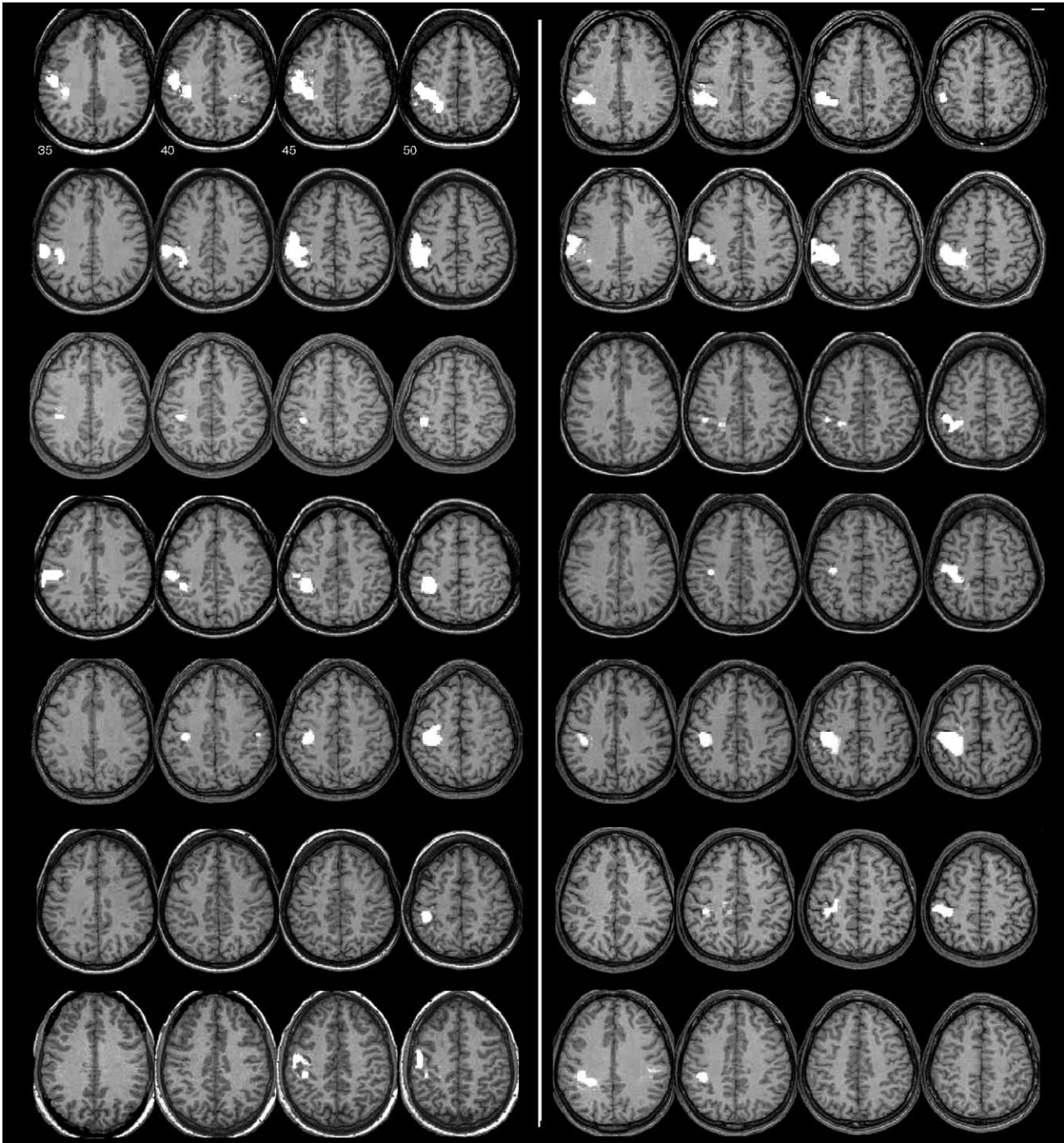
Fig. 4. Localization of grasp-related activity in the anterior parietal region of interest in 14 subjects. Despite substantial variability in cortical topography within this region, peak activation is located at or near the intersection of the intraparietal and postcentral sulci in all 14 subjects.

topography, each of the individuals demonstrates activity at the junction of the left anterior IPS and postcentral sulcus.

5. Discussion

In summary, these findings are consistent with several previous studies suggesting the existence of a functional homologue in the human brain of macaque area AIP. As in the macaque, aIPS is located near the junction of the anterior IPS and postcentral sulcus. In both species this region appears to play a key role in visuomotor transformations involved in grasping and object manipulation. Furthermore, in humans this region is known to be activated when tasks involve viewing, naming [5], or retrieving the actions associated with familiar manipulable objects

[7,25]. These later results suggest that parietal grasp representations may be driven top–down by semantic information [22,24].

Our findings extend this literature in two important ways. First, we show that despite substantial individual variability in cortical topography, visually guided grasping selectively and consistently activates an area located at the junction of the anterior IPS and postcentral sulcus contralateral to the involved hand. Second, we report additional activation in the contralateral parietal operculum (putative SII), suggesting that this area may also play a role in grasping. In macaques, both AIP and SII project heavily to area F5ab [13]. We hypothesize that during grasping human SII is activated in association with available haptic information concerning the objects' shapes.

An important question concerns the cerebral organization of these sensory motor transformations. On the one hand, our finding of left parietal activation may reflect a contralateral organization given that only the right hand was used in these tasks. This fits well with observations demonstrating impaired grasping with the contralateral right hand following lesions to this area in the left hemisphere [1]. However, unimanual haptic exploration and recognition both appear to activate aIPS bilaterally [2,3]. Bilateral activations have also been detected during visually guided grasping in healthy adults [1]. On the other hand, at least in right-handers, the left hemisphere may be dominant for these functions. As evident in Table 1, even visual processing tasks that do not involve overt motor behaviors seem to preferentially activate left aIPs. More work is needed to evaluate the specific task demands related to differences in the laterality of aIPS activity.

A second question concerns our failure to detect significant activation in ventral premotor and/or inferior frontal cortex. In macaques, area F5 contains interleaved representations of the fingers, hands, and mouth [32]. Cells within F5 appear to be involved in the preparation and execution of visually guided grasping actions [33]. This area is subdivided into F5ab—in the posterior bank of the inferior arcuate sulcus and area F5c—located in the dorsal convexity. Both subdivisions receive major inputs from secondary somatosensory cortex (SII), and IPL area PF [13], which also contains a representation of the face and arm. Area F5ab also receives a major projection from AIP. Cells in this region display response properties consistent with the visual, motor, and visual–motor subtypes of neurons in area AIP, and their role in computing the opposition space of visually guided grasping movements has recently been articulated [29]. On the basis of cytoarchitectonic similarities, it has been suggested that macaque area F5 is homologous with pars opercularis in the human inferior frontal cortex [30,31]. Yet, detection of activity in this region during visually guided grasping has been inconsistent, with some studies reporting effects [9,10] and others not [15,16,33]. In addition, Binkofski et al. [2] identified responses in BA44 with haptic manipulation, but not

visually guided grasping. The reasons for these differences remain unclear. One possibility is that the inferior frontal activations are recruited for any goal-oriented task, whereas aIPS is specific to those involving hand affordance [18]. As such, both the control task (pointing to and pushing in the objects) and the grasp task required specific motor goals. Consequently, activations within inferior frontal areas could have cancelled one another when compared. It is also possible that higher field strengths are critical for detecting activity in this brain region [26]. However, we have found activation within these regions at 1.5 T when subjects observe objects being grasped [23].

Acknowledgments

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