RESEARCH ARTICLE

Jody C. Culham · Stacey L. Danckert ·
Joseph F. X. DeSouza · Joseph S. Gati · Ravi S. Menon ·
Melvyn A. Goodale

Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas

Abstract Although both reaching and grasping require transporting the hand to the object location, only grasping also requires processing of object shape, size and orientation to preshape the hand. Behavioural and neuropsychological evidence suggests that the object processing required for grasping relies on different neural substrates from those mediating object recognition. Specifically, whereas object recognition is believed to rely on structures in the ventral (occipitotemporal) stream, object grasping appears to rely on structures in the dorsal (occipitoparietal) stream. We used functional magnetic resonance imaging (fMRI) to determine whether grasping (compared to reaching) produced activation in dorsal areas, ventral areas, or both. We found greater activity for grasping than reaching in several regions, including anterior intraparietal (AIP) cortex. We also performed a standard object perception localizer (comparing intact vs. scrambled 2D object images) in the same subjects to identify the lateral occipital complex (LOC), a ventral stream area believed to play a critical role in object recognition. Although LOC was activated by the objects presented on both grasping and reaching trials, there was no greater activity for grasping compared to reaching. These results suggest that dorsal areas, including AIP, but not ventral areas such as LOC, play a fundamental role in computing object properties during grasping.

J. C. Culham (✉) · S. L. Danckert · J. F. X. DeSouza ·
M. A. Goodale
Department of Psychology, University of Western Ontario,
London, Ontario, N6A 5C2, Canada
e-mail: culham@uwo.ca
Tel.: +1-519-6792111
Fax: +1-519-6613961

J. F. X. DeSouza
Department of Physiology, University of Western Ontario,
London, Ontario, N6A 5C1, Canada

J. S. Gati · R. S. Menon
Advanced Imaging Labs, John P. Robarts Research Institute,
London, Ontario, N6A 5K8, Canada

Keywords fMRI · Grasping · Reaching · Visuomotor control · Parietal cortex

Introduction

Although most research on the visual processing of objects has focused on object recognition, it is important to remember that people also use vision to direct actions towards objects. In fact, one can catch a projectile, such as a tossed apple or a baseball, forming the hand to the appropriate shape and size, regardless of whether or not the object has been recognized. Typically, object recognition and object-directed action do occur together, as when one identifies the apple within a bowl of fruit and then directs the hand to grasp it. Nevertheless, growing evidence suggests that recognition and action rely on distinct and dissociable neural substrates.

Perhaps the most compelling evidence for a dissociation between object recognition and object-directed action comes from neuropsychology. In one striking example, a patient with visual agnosia (D.F.) resulting from occipitotemporal damage shows profound deficits in object recognition but can nonetheless direct well-formed actions towards the same objects (Goodale et al. 1991). Particularly surprising is her preserved ability in grasping to preshape the hand according to the orientation and size of the object to be grasped despite an inability to make perceptual judgements about the object's orientation or size. Conversely, a patient with optic ataxia resulting from parietal lobe damage demonstrates impaired preshaping during grasping but no deficits in object recognition tasks (Jakobson et al. 1991). Although object recognition and grasping both require processing of shape, size and orientation, these processes can clearly be dissociated both in terms of their functions and their neural substrates (Goodale and Milner 1992).

Such evidence has led to the suggestion that visual processing proceeds in two streams: a ventral pathway from occipital to temporal cortex involved in recognition and a dorsal pathway from occipital to parietal cortex

involved in action. Neuroimaging, particularly functional magnetic resonance imaging (fMRI), has identified specific regions within the human ventral and dorsal pathways that likely subserve object recognition and object-directed actions. In the ventral pathway, the lateral occipital complex (LOC) is a large bilateral region of occipitotemporal cortex that is activated by the visual presentation of objects compared to textures or scrambled objects (Malach et al. 1995; Grill-Spector et al. 2001). In the dorsal pathway, the anterior intraparietal (AIP) region responds more strongly during grasping than reaching towards visual objects (Binkofski et al. 1998). This human AIP region is a likely homologue of a region in the macaque monkey containing neurons that respond when the monkey grasps a specific object (Taira et al. 1990; Sakata et al. 1992, 1997). Disruptions to AIP in both the human (Binkofski et al. 1998) and monkey (Gallese et al. 1994) lead to impairments in preshaping the hand for grasping, although reaching remains relatively intact.

We investigated whether brain activation for grasping, compared to reaching, would indeed be limited to dorsal stream areas, with no differential activation in ventral stream cortex, particularly area LOC.[1] We developed a robust paradigm using functional magnetic resonance imaging (fMRI) to study visually guided grasping and reaching. By comparing brain activation for grasping vs. reaching, we identified regions involved in the object-specific "grip" component of the grasp (while subtracting out the "transport" component common to both grasping and reaching) (Jeannerod 1981). In particular, we were able to reliably identify grasp-selective activation in the anterior intraparietal sulcus (see also Culham, in press). In addition, we identified area LOC in the same population of subjects using a standard object perception localizer comparing intact vs. scrambled 2D images of objects (Grill-Spector et al. 2001). We then examined the activation for grasping and reaching in area LOC and the response to 2D object images in AIP.

Materials and methods

Subjects

Seven (four male, three female) young (23–33) subjects participated. All were unambiguously right-handed based on questions from the Edinburgh Handedness Inventory (Oldfield 1971). All subjects were highly experienced in keeping still and maintaining fixation during fMRI experiments. They all had good health, no history of neurological disorders, and normal or corrected (with contact lenses) vision.

Subject configuration

During the grasping and reaching experiments, the subjects were positioned with the head tilted to enable them to look at the targets without mirrors (Fig. 1a) and to reach and grasp target shapes using the right hand. We avoided the use of a mirror because it makes

---

[1] Preliminary results from this study have previously appeared in abstract form (Culham et al. 2001).

action tasks unnatural and may engage a different brain network than would normal actions. Subjects lay supine in the bore of the magnet with the torso slightly tilted by a shallow ramp (5° tilt). Within the cylindrical head coil, the head was tilted (approximately 20–30°) by placing foam wedges underneath. Thus the natural direction of gaze was not directly upward, as in most imaging experiments, but oblique (see Fig. 1). To avoid discomfort from gazing downward through the scans during continuous fixation, we mounted a light-emitting diode (LED; masked by a 0.1° aperture) on the ceiling of the bore, approximately 10° of visual angle above the location of the target. Targets fell within their lower visual field, a configuration that is not unusual in everyday grasping acts. Subjects maintained fixation on the LED which could be illuminated in one of two colors, red or green, calibrated for photometric equiluminance (8 cd/m^2). Although eye movements could not be monitored online at the time these experiments were conducted, we do not believe that eye movements could account for the activation during grasping for several reasons. Namely, all subjects were all highly experienced at maintaining fixation, no grasp-related activation was observed in parietal eye movement areas (e.g., Kawashima et al. 1996; Muri et al. 1996; DeSouza et al. 2000), and it is unlikely that eye movement patterns would differ for grasping and reaching. The subject's resting position was with the hand placed over the navel so as to be comfortable and not restrict the view of the object. Care was taken to minimize the potential for head motion. A semi-cylindrical arm brace with Velcro straps supported and restrained the subject's upper right arm, allowing limited motion at the elbow and full motion at the wrist while restricting shoulder movement and the conduction of arm movements to the head.

Grasping apparatus ("Grasparatus")

Stimuli were composed of translucent white plastic rectangles of constant width (20 mm=2° visual angle) with varying length (20–40 mm=2–4° visual angle) and orientation (a range of approximately 90°, using only orientations that afforded a comfortable precision grasp). Eight different objects were mounted on each face of a rotating octagonal drum, known as the "grasparatus". The target object facing the subject could be illuminated by a computer-controlled super-bright LED (12 cd/m^2) mounted inside the cylinder. In the present experiments, only a single target location was used and the other locations were masked by a piece of cloth. The target object facing the subject changed between trials. To accomplish this, a computer-controlled solenoid released air from a compressor (outside the magnet room) into a hose (going into the magnet room) attached to an elasticized piston that moved the cylinder by 1/8 turn such that the next object in the sequence was on the side facing the subject. The grasparatus was supported on each side by an acrylic bracket with a long plastic stalk. The stalk was placed in a clamp on a horizontal brace supported by two legs that fit into slots in the magnet bed. The brace sat over the subject's thighs and the clamp allowed sufficient translations and rotations to position the grasparatus such that it would be as comfortable as possible to grasp objects at the target location. All of the hardware (target LED, fixation LEDs and pneumatic solenoid) was triggered by a computer (Macintosh G4) that received a signal from the fMRI scanner at the start of each trial.

Event-related timing

To eliminate activation due to visual and motion stimulation, the subject remained in the dark except for a brief illumination of the target. Just prior to a trial, the cylinder would rotate to place the next object facing the subject. Then the target object would be illuminated for 250 ms (to minimize the likelihood of eye movements). Target illumination served as a cue for the subject to begin grasping or reaching immediately, based on the color of the fixation LED: green for grasping, red for reaching. In the grasping condition (G), subjects grasped the long axis of the rectangular

182
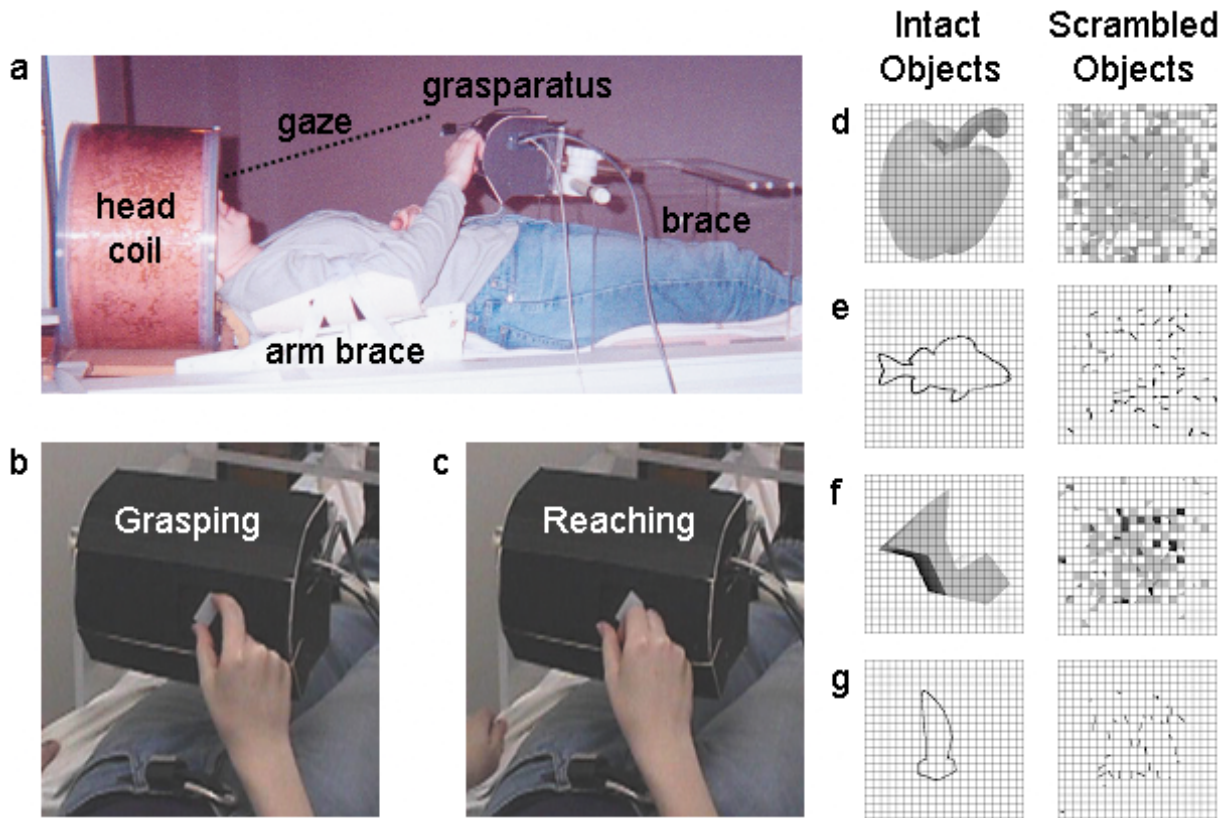
Fig. 1a–g Experimental stimuli. **a** Setup for grasping and reaching experiments. The subject's torso and head were tilted such that the line of gaze was directly above the grasparatus, a rotating drum that was used to present objects which could be grasped with the right hand. **b** In the grasping condition, the subject used a precision grip (finger and thumb) to grasp the long axis of rectangular objects that varied in orientation and length. **c** In the reaching condition, the subject reached to the target location to touch the target with the knuckle without preshaping the hand. **d–g** To identify areas involved in object perception, two-dimensional images of intact objects (*left column*) or scrambled images of the same objects (*right column*) were presented. Pictures could be grayscale images (*rows* **d, f**) or line drawings (*rows* **e, g**) and could be familiar (*rows* **d, e**) or novel (*rows* **f, g**)

target object using a precision grip with the index finger and thumb (Fig. 1b). The objects were firmly mounted on the cylinder, so the subjects did not attempt to lift the object from the cylinder. In the reaching condition (R), subjects transported the arm to the target location, but rather than forming a grip, they touched the object with the knuckles (Fig. 1c). This form of reaching was used because we wished to avoid any shape processing that might be necessary to compute the centroid of the target and any preshaping of the hand in the control condition. After the grasping or reaching action, the subject returned the hand to the resting position and waited until the next trial. Trials were spaced every 14 s, the optimal inter-trial interval for event-related imaging with widely spaced trials (Bandettini and Cox 2000). To reduce cognitive demands caused by frequent task changes, widely spaced trials were presented in blocks of four (e.g., four reach trials, then four grasp trials and so on), alternating between conditions (e.g., RGRGRGR).

Event-related imaging gave us far better data quality than blocked designs. Preliminary experiments using blocked designs found considerable artifacts. These artifacts may have been due to head motion yoked with the arm motion, though they were not eliminated by considerable efforts to stabilize the head (e.g., bite bars). Empirical testing suggested another possible source for the artifacts: distortions of the magnetic field due to the changing position of the arm. To reduce mass-related artifacts, we emphasized to subjects that they must return the hand to the same resting position between trials and do their best not to shift hand or body positions between conditions. We also employed an event-related design to dissociate true activations from spurious signal changes resulting from head movement and/or mass artifacts (Birn et al. 1999). That is, although artifacts occur without a delay, true activation occurs at the standard hemodynamic lag of approximately 5 s and with the characteristic hemodynamic response profile.

Object stimuli

As described in detail elsewhere (Kourtzi and Kanwisher 2000), object stimuli included line drawings or grayscale images of either familiar objects or novel shapes (subtending approximately 20° visual angle) (Fig. 1d–f). Activation was compared during blocks (16 s, 1 item/s) of intact images vs. blocks of scrambled images of the same stimuli. To maintain attention across all stimulus conditions, subjects performed a "1-back" task, hitting the button every time a stimulus was repeated (despite some position jitter). The order of blocks was counterbalanced between subjects.

MR imaging parameters

Blood oxygenation level dependent (BOLD) images were collected with a 4.0-Tesla Siemens-Varian MRI system (Erlangen Germany; Palo Alto, CA) using a head coil. Two sessions were conducted, one for grasping, one for object presentation. In each session, 13 slices were aligned approximately parallel to the calcarine sulcus to sample occipital, occipitotemporal and posterior parietal cortex with a slice thickness of 6 mm and an in-plane resolution of 3 mm (field of view 19.2 cm, 64×64 matrix). Each volume (13 slices) was sampled once every 2.0 s. Functional data were collected using T2*-weighted segmented gradient echo echoplanar imaging (TE=20 ms,

TR=1000 ms, flip angle=45°, 2 segments/plane, navigator-corrected). T1-weighed anatomical images were collected with the same slice orientation (three dimensional magnetization-prepared (MP) turbo FLASH acquisition with inversion time (TI)=500 ms, echo time (TE)=6 ms, repetition time (TR)=11 ms, flip angle=11°, 256×256 matrix ×64 slices, 0.75 mm×0.75 mm×3 mm voxels).

Data analysis

Data were analyzed using Brain Voyager software (Brain Innovation, Maastricht, Netherlands). For each subject, anatomical and functional data from each session were realigned to a "canonical" session in which the gray-white matter boundary had been segmented to generate a cortical surface which could then be rendered in 3D and inflated. Each canonical brain, and the realigned functional data, was transformed into stereotaxic space (Talairach and Tournoux 1988). Functional data were screened for motion or magnet artifacts with cine-loop animation. No head motion artifacts were observed, likely because our subjects were highly experienced, so no motion correction was applied (Freire and Mangin 2001). Functional data were preprocessed with linear trend removal, spatial smoothing (FWHM=4 mm) and temporal smoothing (FWHM=3 images). Data were analyzed using a general linear model (GLM) with separate predictors for each state, convolved with the hemodynamic response function and contrasts between the predictors (e.g., +Grasp, −Reach; and +Intact Objects, −Scrambled Objects). GLM data could be analyzed across the whole group (in stereotaxic space) or for individual subjects.

Results

We first identified two regions of interest (ROIs) based on standard task comparisons: AIP was identified by object grasping (vs. reaching) and LOC was identified by object (vs. scrambled image) perception. For each region, time courses were extracted from the group average data (after transformation into Talairach space) and from each individual subject. Consistency of activation patterns across subjects was assessed by performing two-tailed paired t-tests on activation levels extracted from time course data for each subject within a given ROI.

After identifying each ROI using the primary task comparisons, we then evaluated the activity of each region in the secondary task (i.e., AIP activity in intact vs. scrambled objects; LOC activity in grasping vs. reaching). We began by examining activation maps for regions of overlap between the primary and secondary task. No such overlap was observed. We then performed a further analysis of single subject ROI data (using $p<.05$) to ensure that any null results reported in the group analyses were indeed due to a lack of activation differences in the secondary task, not simply individual variability in regional activation or the conservative statistical testing required for activation maps involving many voxelwise comparisons.

Activation in AIP during grasping

The comparison of grasping vs. reaching produced activation in the anterior end of the intraparietal sulcus. In the group analysis, three foci were observed: one in the left hemisphere at the junction of the intraparietal sulcus (IPS) and postcentral sulcus (PostCS) and two symmetric regions, one in each hemisphere, in the anterior IPS, posterior to its junction with the PostCS (Figs. 2a, 3b). As seen in the event-related time course data in Fig. 4a, all three areas responded during both reaching and grasping, but significantly more during grasping. The more anterior region at the IPS/PostCS junction appeared only in the left
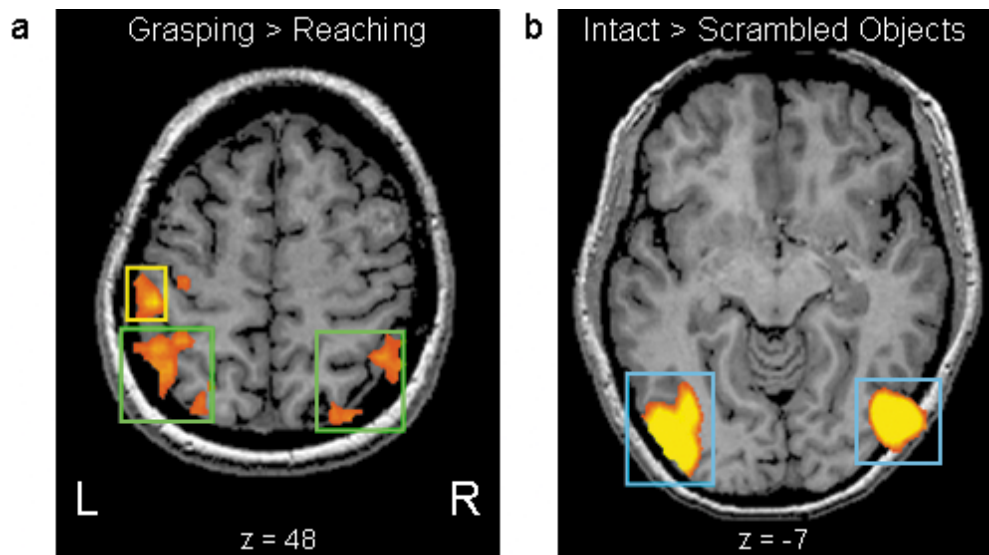
Fig. 2a, b Group activation maps for object grasping and object perception. a Three parietal regions were more active for grasping than reaching: one focus (*yellow box*) in the postcentral sulcus of the left hemisphere, and two more posterior bilateral foci (*green boxes*) in the intraparietal sulcus ($t_{(2896)}>4.0$, $p<.0001$ uncorrected, cluster size >100 mm³). Although the AIP activation appears to consist of two foci, these were contiguous in other slices. b The comparison between intact and scrambled objects activated bilateral foci in lateral occipital cortex ($t_{(2506)}>4.0$, $p<.0001$ uncorrected, cluster size >100 mm³). Data are based on Talairach averaged group results shown for clarity on a single subject's anatomical (which is not representative of the sulcal patterns for all subjects)

hemisphere, contralateral to the hand used for grasping. Other experiments from our lab (Culham, in press) have suggested that activation in the more anterior focus is likely related to the somatosensory aspects of the task; whereas, the more posterior foci have visual, as well as somatosensory responses, consistent with responses expected from monkey AIP (Taira et al. 1990). Thus, we will tentatively refer only to our more posterior foci in the anterior IPS as AIP.

Bilateral activation in the anterior IPS was observed in all seven subjects, with the exception of one subject (Subject 7) in whom no right IPS activation was detected. Data from the left hemisphere of one representative subject are shown in Fig. 3. Within individuals, it was not always possible to distinguish the left hemisphere PostCS and IPS activations, so the two regions were grouped together for the single subject analyses. As expected from the statistical tests used to define the regions, a significantly greater response for grasping compared to reaching was observed in both the left PostCS/IPS and right IPS foci ($p<.05$; Fig. 4a). In each hemisphere, the responses to reaching and grasping were both significantly greater than the inter-trial baseline ($p<.05$; Fig. 4a).

Activation in LOC during object perception

The subtraction of intact minus scrambled objects produced a large, bilateral activation in lateral occipital and ventral occipitotemporal cortex, consistent with earlier studies. As expected from the statistical tests used to define the LOC, a significantly greater response for intact compared to scrambled objects was observed in lateral occipital cortex in both the left and right hemispheres ($p<.001$, two-tailed; Fig. 2b). A continuous zone of activation was seen in both the dorsal lateral occipital lobes and the ventral-posterior fusiform area, which together comprise the LOC (Malach et al. 2002). Because it is not yet clear what subdivisions may be included within this vicinity (Grill-Spector et al. 2001), the entire object-selective zone was taken to be LOC in these experiments. The response to intact objects was significantly greater than to the fixation baseline in both the left ($p<.001$) and right ($p<.01$) hemispheres (Fig. 4d). All seven individual subjects had a focus of activation in the lateral occipital cortex of each hemisphere (including one typical subject's data shown in Fig. 1c).
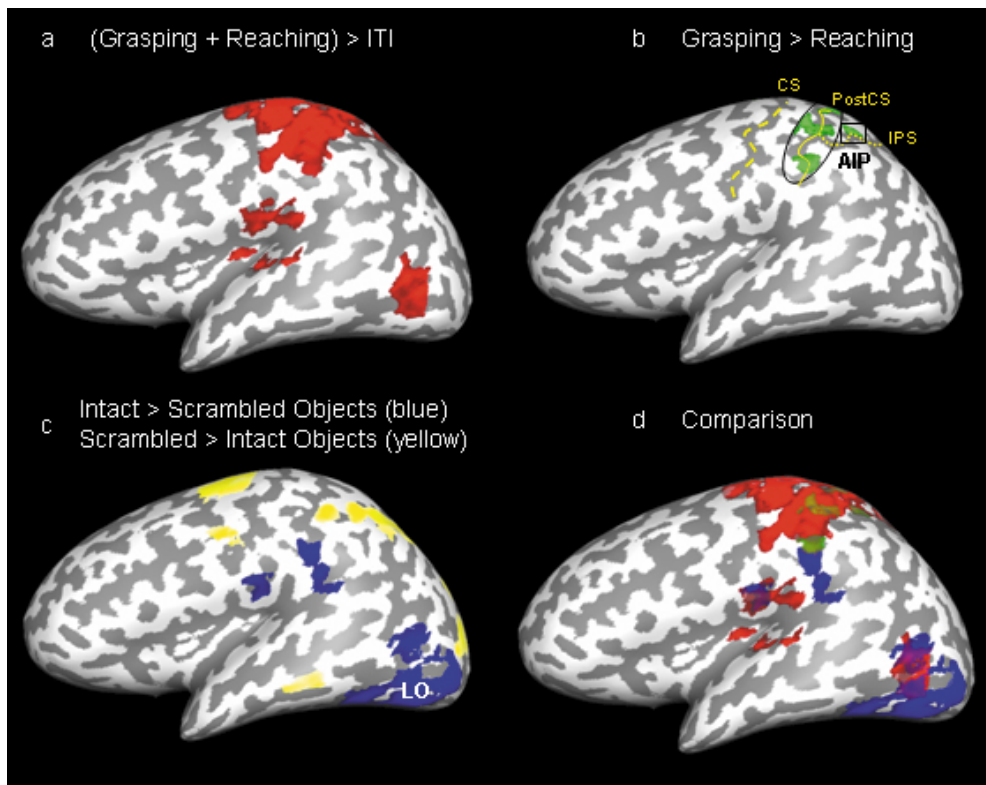
Fig. 3a–d Activation for a single representative subject shown on an inflated cortical surface. **a** Event-related activation for grasping and reaching compared to the intertrial interval (*ITI*) shown in red ($t_{(2884)}>4.0$, $p<.0001$ uncorrected, cluster size >100 mm^3). Data are rendered on an inflated cortical left hemisphere (*dark gray* sulci, *light gray* gyri). **b** Areas with significantly greater activation for grasping than reaching included the postcentral sulcus (*PostCS*) and anterior intraparietal sulcus (*IPS*) shown in *green*. Sulci are shown with *dotted lines* and include the central sulcus (*CS*) for comparison. **c** The lateral occipital (*LOC*) complex was significantly more active during viewing of intact than scrambled objects (*blue*). Some subjects, including this one, also had activation in the posterior Sylvian fissure. The reverse comparison, scrambled >intact, shown in *yellow*, activated the intraparietal sulcus and, in this subject, frontal eye fields. **d** For comparison, activation for reaching and grasping (*red*), grasping-reaching (*green*) and intact-scrambled (*blue*) are shown in transparent color. *Yellow* indicates the overlap between grasping and reaching data. *Purple* indicates overlap between reaching and grasping and intact-scrambled
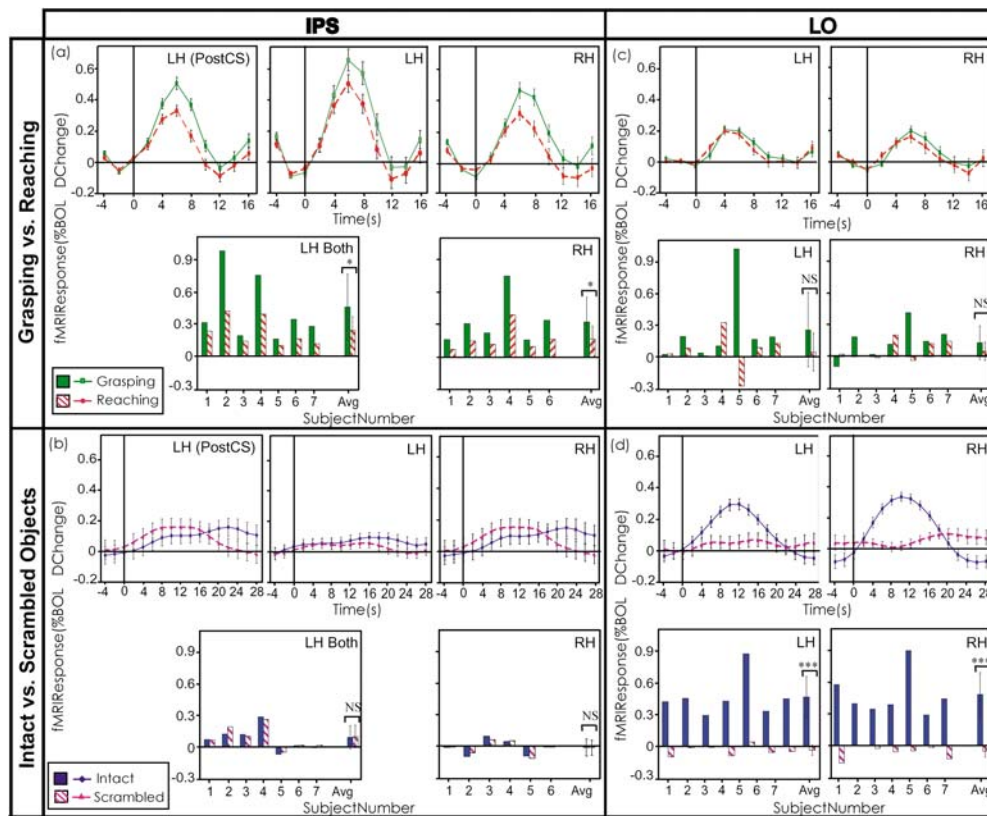
Fig. 4a–d Activation in AIP and LOC during grasping vs. reaching and viewing of intact vs. scrambled objects. **a** Activation in three parietal regions, the left IPS/PostCS junction, the left IPS (posterior to the junction with the PostCS), and the right IPS during visually guided grasping (*green*) and reaching (*red*). *Line graphs* indicate the event-related average time courses of activity for the three group-defined regions of interest with time 0 indicating the start of the trial (grasping vs. reaching) or the start of the 16-s stimulus epoch (intact vs. scrambled objects). *Error bars on line graphs* show standard error of the mean. *Bar graphs* display the average magnitude of activation for the peak four volumes (4–10 s after each trial began) for a region of interest selected individually for each subject. Not all subjects showed a clear dissociation between the left PostCS and left IPS regions, so the two left hemisphere regions have been grouped together in the bar graph. One subject showed no activity in the right

IPS and was excluded from the right IPS bar graphs in **a** and **b**. The *rightmost bar in each graph* shows the group average with error bars indicating the 95% confidence limits (to facilitate comparisons with 0) and the comparison bracket indicating the significance of the difference between the two conditions (*$p<.05$, ***$p<.001$, *NS* non-significant). **b** Time course and activation level graphs (as in **a**) for the analysis of parietal regions in the comparison between viewing intact objects (*blue*) and scrambled objects (*pink*). Activation levels were computed from the peak four volumes (8–14 s after each block began). **c** Time course and activation level graphs (as in **a**) for the analysis of left and right hemisphere LOC regions in the comparison of grasping and reaching. **d** Time course and activation level graphs (as in **a**) for the analysis of left and right hemisphere LOC regions in the comparison between viewing intact and scrambled objects

Activation in AIP during object perception

Activation in AIP was examined for the comparison between images of intact vs. scrambled objects. A slightly greater response to scrambled than intact objects was observed in the Talairach-averaged group data. In the single subject ROI analyses (Fig. 4b), however, the differences were far from significant in either the left ($p=.42$) or the right hemisphere ($p=.87$). In no case did the response to either scrambled or intact objects differ significantly from the fixation baseline. Subsequent analyses suggested that there were no significant effects of object categories (novel vs. familiar objects; grayscale images vs. line drawings) on AIP activation levels.

Activation in LOC during grasping

Activation in LOC was examined for the comparison between grasping vs. reaching. Within the group data (Fig. 4c, upper panels), an LOC response was clearly visible for both grasping and reaching, with little difference between the two conditions. In the single subject analyses (Fig. 4c, bar graphs in lower panels), the difference between grasping and reaching was not significant in the left ($p=.35$) or right ($p=.31$) hemispheres and appeared to be largely due to an anomalous result in one subject (Subject 5). Although the peak responses in LOC for grasping and reaching were higher than the intertrial baseline for the majority of subjects, these responses were not significantly greater than the baseline in the single subject analysis. To ensure that grasping-specific activation was not simply limited to a subregion of LOC, we also examined the contrast between grasping and reaching

Table 1 Areas significantly more activated by intact than scrambled images ($t_{(2506)} > 4.0$, $p < .0001$ uncorrected, cluster size > 100 mm^3). At the strictest Bonferroni correction for multiple comparisons ($t_{(2096)} > 4.72$, 19,882 functional voxels, $p < .05$ corrected), all regions remain significantly activated

Region	t value	Volume (mm^3)	x	y	z
Left LOC	12.6	16,103	−42	−70	− 8
Right LOC	14.1	9,433	47	−71	− 7
Left superior temporal gyrus	6.6	881	−59	−50	12
Left posterior Sylvian	5.6	763	−54	−36	20
Right middle temporal gyrus	6.1	195	46	−64	10

and found no significant activation within any part of LOC.

Activation in other areas

In addition to LOC, the comparison of intact minus scrambled images also produced group activation in three additional areas, the left superior temporal sulcus, the right middle temporal gyrus, and the left posterior Sylvian fissure. Talairach coordinates are specified in Table 1.

The reverse comparison, scrambled minus intact images, yielded a continuous swath of activation throughout almost the entire IPS (posterior to the PostCS) and the posterior occipital cortex (e.g., Fig. 3C, yellow). Due to the extent and contiguity of this region, no attempt was made to report Talairach coordinates. This extensive activation is likely related to the use of a "1-back" task to control attention, which subjects reported as qualitatively more difficult in the scrambled than intact condition.

The comparison of grasping minus reaching produced additional areas of bilateral activation, including frontal eye fields, visual cortex, and the thalamus (according to the Talairach coordinates, thalamic activity was in the ventral posterolateral/posteromedial nuclei, which have projections to somatosensory and motor cortex). In addition, activity was observed in only the left hemisphere

Table 2 Areas significantly more activated by grasping than reaching ($t_{(2896)} > 4.0$, $p < .0001$ uncorrected, cluster size > 100 mm^3). At the strictest Bonferroni correction for multiple comparisons ($t_{(2896)} > 4.8$, 30,258 functional voxels, $p < .05$ corrected), all regions remain significantly activated except the left thalamus

Region	t value	Volume (mm^3)	x	y	z
Left PostCS	7.3	2,638	−50	−27	44
Left AIP	6.6	3,184	−38	−48	52
Right AIP	6.7	3,368	40	−50	50
Left thalamus	5.6	661	−14	−21	7
Right thalamus	5.5	391	12	−17	10
Left FEF	6.0	238	−30	−11	61
Right FEF	6.5	1,441	29	−10	63
Left M1	7.2	1,115	−29	−18	56
Left parieto-occipital cortex	6.4	1,700	−17	−73	32
Left posterior cingulate	6.2	594	−12	−33	40
Visual areas	8.3	13,944	5	−78	3

for motor cortex, parieto-occipital cortex and the posterior cingulate. Talairach coordinates are specified in Table 2. No areas were significantly ($t > 4.0$) more active for reaching than grasping. None of the areas activated by grasping (minus reaching) was activated by intact objects more than scrambled or more than the baseline.

Trial-related activation for both reaching and grasping (compared to the intertrial interval) was observed throughout a wide continuous region that included frontal eye fields (bilateral), motor cortex (left), and postcentral (mostly left) and intraparietal sulci (bilateral, stronger on the left), as well as supplementary motor areas and the cingulate sulcus (medial), the thalamus (bilateral), posterior Sylvian (bilateral, stronger on the left), parieto-occipital cortex (bilateral), lateral occipital cortex (bilateral), and intermediate (peripheral) visual areas (medial). Due to the extent and contiguity of many of these regions, no attempt was made to report Talairach coordinates. No areas were significantly ($t < −4.0$) deactivated during reaching and grasping.

Discussion

Taken together, our results support the suggestion that information regarding object shape is processed independently along two pathways, the dorsal and ventral streams (Goodale and Milner 1992). First, we have found an area in the anterior intraparietal sulcus, human AIP, that is activated when object size and shape computations are required to preshape the hand during grasping, as compared to reaching which does not require preshaping. Human AIP showed no response to 2D images of objects for which no grasping response was required. Second, within area LOC, a well-characterized object-processing area in the ventral stream, we have demonstrated weak responses to target objects for motor actions (significant in group but not single subject analyses), but no differential response for the object computations required for grasping. These results support the suggestion that the computations of object properties for recognition purposes and hand preshaping occur independently within the dorsal and ventral streams.

Our results highlight a new area within the dorsal stream, AIP, that appears, as with a similar area in the monkey (Taira et al. 1990), specialized to compute object properties in order to preshape the hand during grasping.

Such an area has been suggested in the earlier human neuroimaging literature, but the results have been mixed. Activation within the postcentral and/or anterior intraparietal regions has been reported in two experiments examining visually guided grasping vs. reaching (Faillenot et al. 1997b; Binkofski et al. 1998), one experiment contrasting grasping vs. a visual control condition (Rizzolatti et al. 1996) and several experiments examining non-visual grasping (Ehrsson et al. 2000; Kinoshita et al. 2000; Kuhtz-Buschbeck et al. 2001). However, two early positron emission tomography (PET) studies of grasping (vs. reaching) did not report AIP activity (Grafton et al. 1996; Matsumura et al. 1996). We attribute the reliability of our AIP results (seen in 7/7 subjects in the left hemisphere and 6/7 in the right hemisphere) to the development of a robust event-related experimental fMRI paradigm to study grasping with high-field fMRI. We were particularly careful to ensure that subjects acted toward a variety of objects (unlike some previous studies that presented a very limited number of stimuli due to space constraints), that motion artifacts could not contaminate the data, and that the motor tasks differed only on the addition of a hand preshaping/grasping component (with minimal differences in visual aspects because hand movements occurred in the dark). Other studies from our lab (Culham, in press) suggest a critical role for AIP in visually guided grasping. In particular, studies of delayed grasping have demonstrated both an AIP response (within the anterior IPS but not PostCS) at the time of visual presentation of an object and at the time the action is initiated (Culham et al. 2001). Furthermore, AIP activation is higher for grasping than reaching during both the vision and action phases of the trial. These properties are consistent with those expected from data on monkey area AIP (Taira et al. 1990) which contains subpopulations that respond to the visual stimulus only, the grasping action only, or optimally when the object is both seen and grasped.

Unlike AIP, no ventral stream areas, not even LOC, demonstrated a significantly greater response to grasping than reaching. These results suggest that AIP, likely in conjunction with other areas in parietal and frontal cortex, computes object properties for the purposes of action with no need for additional processing required in the ventral stream area LOC. This conjecture is supported by our recent fMRI studies of patient D.F. to investigate which regions subserve her spared grasping abilities despite profound deficits in object recognition (James et al., in press; Steeves et al., submitted). Structural MRI revealed that D.F.'s ventral stream lesions clearly overlap with the expected location of LOC in normals, with only a small portion in the vicinity of the fusiform face area spared (James et al., in press; Steeves et al., submitted). Despite the absence of processing in LO, D.F. can nevertheless accurately perform grasping actions and shows activation in area AIP. Thus it seems that LOC is neither activated by, nor necessary for, object grasping.

It is possible that frontal areas, particularly premotor cortex, may also be involved in the control of object-directed grasping. In the macaque monkey, ventral premotor area F5 receives input from AIP and sends output to motor cortex (M1) (Matelli et al. 1986) and contains neurons with object grasping properties similar to AIP (Rizzolatti et al. 1988; Fogassi et al. 2001). Unfortunately our slice selection to sample both AIP and LOC included only the most superior and posterior regions of frontal cortex (around the frontal eye fields) and did not include more anterior or inferior regions such as Broca's area (Brodmann's area 44) which has been suggested as a possible human homologue of monkey F5 (Rizzolatti and Arbib 1998).

We found no evidence of activation in AIP for viewing of 2D images; however, that is not to say that AIP may never be activated by real objects or object images. Rather, AIP may be a multimodal area that encodes object shape in 3D space for action planning and manipulation rather than for recognition per se. If the area we have identified here is in fact the human homologue of monkey AIP, like monkey AIP, it should also respond to the presentation of graspable 3D objects even when no grasping action is executed (Taira et al. 1990). Indeed, one PET study reported significant activation of an area near our putative AIP during grasping (vs. reaching) and near-significant activation of the same area during a task which involved matching 3D objects (Faillenot et al. 1997b). Activation in this vicinity has also been reported for tactile exploration of complex objects (Roland et al. 1998; Binkofski et al. 1999; Bodegard et al. 2001) and is said to be particularly strong for crossmodal matching of object shapes (between the visual and tactile modalities) compared to intramodal matching of object shapes (within vision or within touch) (Grefkes et al. 2002). In addition, anterior intraparietal activation has been reported for numerous visual tasks in which no direct action was required, including surface orientation discrimination (Shikata et al. 2001), viewing of manipulable tools (Chao and Martin 2000) and maintaining manipulable objects in working memory (Mecklinger et al. 2002). Although the tasks that activate AIP are somewhat heterogeneous, they all involve object-processing functions that would be necessary for acting toward real objects in acts such as grasping, tool use, or tactile exploration. Our present results, however, clearly show that the mere visual presentation of any object—2D objects in this case—is not sufficient to activate AIP.

Even in an attentionally demanding 1-back task, images of objects were insufficient to activate AIP significantly above a fixation baseline. By comparison, performance of a 1-back task on the scrambled images yielded activation throughout the intraparietal sulcus, suggesting a role for these areas in either attention or spatial processing, both of which were more demanding in the scrambled than intact conditions. Nevertheless, we do not believe that the activation in AIP for grasping compared to reaching can be accounted for by attention. First, patients with lesions in this area show highly specific deficits on grasping but not other tasks such as reaching (Binkofski et al. 1998), indicating that AIP is crucial to grasping. Second, AIP activation was highly consistent between observers, yet no

other areas within the intraparietal sulcus were systematically activated, including more posterior regions, which are reliably activated during visually difficult tasks (Wojciulik and Kanwisher 1999). Although the frontal eye fields were activated by reaching, and more so by grasping, recent neurophysiological evidence has suggested that a subpopulation of neurons in FEF is activated during arm movements (Lawrence and Snyder 2002).

In addition to AIP, we also found a grasp-related region in parieto-occipital cortex. This activation appeared to be in the fundus of the superior parieto-occipital sulcus and/or along the caudal intraparietal sulcus, two sulci separated by only a few mm. Activation only reached significance in the left hemisphere, although comparable activity in the right hemisphere could be observed at lower thresholds (t=3.6). A similar region was reported in other studies of grasping (Faillenot et al. 1997b), object viewing (Faillenot et al. 1997a, 1999), and surface orientation discrimination (Faillenot et al. 2001; Shikata et al. 2001) in humans. This activation in the human IPS may be homologous with a monkey area in the caudal intraparietal sulcus (cIPS) which appears to process surface orientation and provides input to AIP (Shikata et al. 1996; Sakata et al. 1997, 1999). Alternatively, activation in the superior parieto-occipital sulcus may correspond to the suggested human homologue of the parietal reach region (Connolly et al. 2003) which, in the monkey, may play a role in grasping (Battaglini et al. 2002).

In sum, we have found that although object grasping and object perception both involve processing of object properties such as shape, size and orientation, they rely on different underlying neural substrates, likely due to the different computational requirements of the two types of object processing. Parietal area AIP is activated more strongly by grasping, when object information is required to preshape the hand, but does not respond to images of objects in the absence of an action. In contrast, temporal area LOC is activated more strongly by objects than scrambled control images, but shows no enhanced activity when real objects are the targets for grasping compared to reaching. These differential activation patterns support and complement earlier work from behavioural and neuropsychological techniques showing a similar dissociation.

References

Bandettini PA, Cox RW (2000) Event-related fMRI contrast when using constant interstimulus interval: theory and experiment. Magn Reson Med 43:540–548

Battaglini PP, Muzur A, Galletti C, Skrap M, Brovelli A, Fattori P (2002) Effects of lesions to area V6A in monkeys. Exp Brain Res 144:419–422

Binkofski F, Dohle C, Posse S, Stephan KM, Hefter H, Seitz RJ, Freund H-J (1998) Human anterior intraparietal area subserves prehension. Neurology 50:1253–1259

Binkofski F, Buccino G, Stephan KM, Rizzolatti G, Seitz RJ, Freund HJ (1999) A parieto-premotor network for object manipulation: evidence from neuroimaging. Exp Brain Res 128:210–213

Birn RM, Bandettini PA, Cox RW, Shaker R (1999) Event-related fMRI of tasks involving brief motion. Hum Brain Mapp 7:106–114

Bodegard A, Geyer S, Grefkes C, Zilles K, Roland PE (2001) Hierarchical processing of tactile shape in the human brain. Neuron 31:317–328

Chao LL, Martin A (2000) Representation of manipulable man-made objects in the dorsal stream. Neuroimage 12:478–484

Connolly J, Andersen RA, Goodale MA (2003) fMRI evidence for a 'parietal reach region' in human brain. Exp Brain Res DOI 10.1007/s00221-003-1587-1

Culham J (in press) Human brain imaging reveals a parietal area specialized for grasping. In: Kanwisher N, Duncan J (eds) Attention and performance XX: functional neuroimaging of human cognition. Oxford University Press, Oxford

Culham JC, DeSouza JFX, Woodward S, Kourtzi Z, Gati JS, Menon RS, Goodale MA (2001) Visually-guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. J Vision 1:194

DeSouza JF, Dukelow SP, Gati JS, Menon RS, Andersen RA, Vilis T (2000) Eye position signal modulates a human parietal pointing region during memory-guided movements. J Neurosci 20:5835–5840

Ehrsson HH, Fagergren A, Jonsson T, Westling G, Johansson RS, Forssberg H (2000) Cortical activity in precision- versus power-grip tasks: an fMRI study. J Neurophysiol 83:528–536

Faillenot I, Sakata H, Costes N, Decety J, Jeannerod M (1997a) Visual working memory for shape and 3D-orientation: a PET study. Neuroreport 8:859–862

Faillenot I, Toni I, Decety J, Gregoire MC, Jeannerod M (1997b) Visual pathways for object-oriented action and object recognition: functional anatomy with PET. Cereb Cortex 7:77–85

Faillenot I, Decety J, Jeannerod M (1999) Human brain activity related to the perception of spatial features of objects. Neuroimage 10:114–124

Faillenot I, Sunaert S, Van Hecke P, Orban GA (2001) Orientation discrimination of objects and gratings compared: An fMRI study. Eur J Neurosci 13:585–596

Fogassi L, Gallese V, Buccino G, Craighero L, Fadiga L, Rizzolatti G (2001) Cortical mechanism for the visual guidance of hand grasping movements in the monkey: A reversible inactivation study. Brain 124:571–586

Freire L, Mangin JF (2001) Motion correction algorithms may create spurious brain activations in the absence of subject motion. Neuroimage 14:709–722

Gallese V, Murata A, Kaseda M, Niki N, Sakata H (1994) Deficit of hand preshaping after muscimol injection in monkey parietal cortex. Neuroreport 5:1525–1529

Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. Trends Neurosci 15:20–25

Goodale MA, Milner AD, Jakobson LS, Carey DP (1991) A neurological dissociation between perceiving objects and grasping them. Nature 349:154–156

Grafton ST, Fagg AH, Woods RP, Arbib MA (1996) Functional anatomy of pointing and grasping in humans. Cereb Cortex 6:226–237

Grefkes C, Weiss PH, Zilles K, Fink GR (2002) Crossmodal processing of object features in human anterior intraparietal cortex: an fMRI study implies equivalencies between humans and monkeys. Neuron 35:173–184

Grill-Spector K, Kourtzi Z, Kanwisher N (2001) The lateral occipital complex and its role in object recognition. Vision Res 41:1409–1422

Jakobson LS, Archibald YM, Carey DP, Goodale MA (1991) A kinematic analysis of reaching and grasping movements in a patient recovering from optic ataxia. Neuropsychologia 29:803–809

James TW, Culham JC, Humphrey GK, Milner AD, Goodale MA (in press) fMRI evidence for a neurological dissociation between perceiving objects and grasping them. Brain

Jeannerod M (1981) Intersegmental coordination during reaching at natural visual objects. In: Long J, Baddeley A (eds) Attention and performance IX. Erlbaum, Hillsdale NJ, pp 153–168

Kawashima R, Naitoh E, Matsumura M, Itoh H, Ono S, Satoh K, Gotoh R, Koyama M, Inoue K, Yoshioka S, Fukuda H (1996) Topographic representation in human intraparietal sulcus of reaching and saccade. Neuroreport 7:1253–1256

Kinoshita H, Oku N, Hashikawa K, Nishimura T (2000) Functional brain areas used for the lifting of objects using a precision grip: a PET study. Brain Res 857:119–130

Kourtzi Z, Kanwisher N (2000) Cortical regions involved in perceiving object shape. J Neurosci 20:3310–3318

Kuhtz-Buschbeck JP, Ehrsson HH, Forssberg H (2001) Human brain activity in the control of fine static precision grip forces: an fMRI study. Eur J Neurosci 14:382–390

Lawrence BM, Snyder LH (2002) Effector specific and non-specific activity in frontal eye fields. Soc Neurosci Abstr:622.628

Malach R, Reppas JB, Benson RR, Kwong KK, Jiang H, Kennedy WA, Ledden PJ, Brady TJ, Rosen BR, Tootell RBH (1995) Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. Proc Natl Acad Sci U S A 92:8135–8139

Malach R, Levy I, Hasson U (2002) The topography of high-order human object areas. Trends Cogn Sci 6:176–184

Matelli M, Camarda R, Glickstein M, Rizzolatti G (1986) Afferent and efferent projections of the inferior area 6 in the macaque monkey. J Comp Neurol 251:281–298

Matsumura M, Kawashima R, Naito E, Takahashi T, Satoh K, Yanagisawa T, Fukuda H (1996) Changes in rCBF during grasping in humans examined by PET. Neuroreport 7:749–752

Mecklinger A, Gruenewald C, Besson M, Magnie MN, Von Cramon DY (2002) Separable neuronal circuitries for manipulable and non-manipulable objects in working memory. Cereb Cortex 12:1115–1123

Muri RM, Iba-Zizen MT, Derosier C, Cabanis EA, Pierrot-Deseiligny C (1996) Location of the human posterior eye fields with functional magnetic resonance imaging. J Neurol Neurosurg Psychiatry 60:445–448

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh handedness inventory. Neuropsychologia 9:97–113

Rizzolatti G, Arbib MA (1998) Language within our grasp. Trends Neurosci 21:188–194

Rizzolatti G, Camarda R, Fogassi L, Gentilucci M, Luppino G, Matelli M (1988) Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. Exp Brain Res 71:491–507

Rizzolatti G, Fadiga L, Matelli M, Bettinardi V, Paulesu E, Perani D, Fazio F (1996) Localization of grasp representations in humans by PET: 1. Observation versus execution. Exp Brain Res 111:246–252

Roland PE, O'sullivan B, Kawashima R (1998) Shape and roughness activate different somatosensory areas in the human brain. Proc Natl Acad Sci U S A 95:3295–3300

Sakata H, Taira M, Mine S, Murata A (1992) Hand-movement-related neurons of the posterior parietal cortex of the monkey: their role in the visual guidance of hand movements. In: Caminiti R, Johnson PB, Burnod Y (eds) Control of arm movement in space: neurophysiological and computational approaches. Springer, Heidelberg, pp 185–198

Sakata H, Taira M, Kusunoki M, Murata A, Tanaka Y (1997) The TINS lecture. The parietal association cortex in depth perception and visual control of hand action. Trends Neurosci 20:350–357

Sakata H, Taira M, Kusunoki M, Murata A, Tsutsui K, Tanaka Y, Shein WN, Miyashita Y (1999) Neural representation of three-dimensional features of manipulation objects with stereopsis. Exp Brain Res 128:160–169

Shikata E, Tanaka Y, Nakamura H, Taira M, Sakata H (1996) Selectivity of the parietal visual neurones in 3D orientation of surface of stereoscopic stimuli. Neuroreport 7:2389–2394

Shikata E, Hamzel F, Glauche V, Knab R, Dettmers C, Weiller C, Buchel C (2001) Surface orientation discrimination activates caudal and anterior intraparietal sulcus in humans: An event-related fMRI study. J Neurophysiol 85:1309–1314

Steeves JKE, Humphrey GK, Culham JC, Menon RS, Milner AD, Goodale MA (submitted) Behavioral and neuroimaging evidence for a contribution of color information to scene recognition in a patient with impaired form recognition

Taira M, Mine S, Georgopoulos AP, Murata A, Sakata H (1990) Parietal cortex neurons of the monkey related to the visual guidance of hand movement. Exp Brain Res 83:29–36

Talairach J, Tournoux P (1988) Co-planar stereotaxic atlas of the human brain. Thieme Medical Publishers, New York

Wojciulik E, Kanwisher N (1999) The generality of parietal involvement in visual attention. Neuron 23:747–764