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Orientation sensitivity to graspable objects: An fMRI adaptation study

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It has been proposed that vision-for-perception and vision-for-action are subserved by distinct streams of visual processing, the ventral and dorsal stream, respectively [Milner, A. D., Goodale, M. A., 1995. The visual brain in action. Oxford University Press, Oxford]. Such a distinction has been supported by a recent functional magnetic resonance (fMR) adaptation study [Valyear, K. F., Culham, J. C., Sharif, N., Westwood, D., Goodale, M. A., 2006. A double dissociation between sensitivity to changes in object identity and object orientation in the ventral and dorsal visual streams: A human fMRI study. Neuropsychologia 44, 218–228], which demonstrated selectivity to object identity but not object orientation within the ventral stream, and selectivity to object orientation but not object identity within the dorsal stream. These results were interpreted as suggesting that changes to object identity (but not to orientation) would alter the representation of the stimulus in the perceptual/recognition system, whereas changes in object orientation (but not necessarily identity) would alter the coding of the stimulus within a visuomotor system concerned with behaviour such as grasping. If orientation sensitivity in the dorsal stream does reflect such a potential for action, then this sensitivity should be specific to graspable objects. Using an fMR adaptation paradigm, we presented participants with an image of either a graspable or non-graspable stimulus, followed by the same image in either the original orientation or its mirror image. One region within the dorsal stream, the lateral occipito-parietal junction (lOPJ), was shown to be sensitive to orientation changes for graspable stimuli; this region did not show orientation sensitivity for non-graspable stimuli. Thus, it appears that the sensitivity to orientation changes in this region is specific to graspable objects, presumably because such changes affect the affordances of graspable but not non-graspable objects.
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Introduction

Goodale and Milner (Goodale and Milner, 1992, 2004; Milner and Goodale, 1995) proposed that perception and visually guided action are subserved by two distinct cortical visual systems. On this view, the ventral stream projecting from striate cortex to inferotemporal cortex is concerned with the perceptual identification of objects, whereas the dorsal stream projecting from striate cortex to posterior parietal cortex mediates the visuomotor transformations required for the online control of actions. Evidence in support of such a distinction has come from work with patients with optic ataxia (reaching deficits that occur following damage to the dorsal stream) (Perenin and Vighetto, 1988; Goodale et al., 1994; Schindler et al., 2004) and visual form agnosia (recognition deficits that occur following damage to the ventral stream) (Goodale et al., 1991, 1994; Milner et al., 1991; James et al., 2003; Rice et al., 2006a). More recently, evidence in support of the distinction between the two streams has been obtained from functional magnetic resonance imaging (fMRI) of healthy subjects. In the ventral stream, the lateral occipital complex (LOC) has been shown to be involved in object processing (for a review, see Malach et al., 2002; Grill-Spector, 2003). In the dorsal stream, on the other hand, areas in and around the intraparietal sulcus (IPS) have been shown to be involved in visually guided eye movements, grasping and reaching (for a review, see Culham and Kanwisher, 2001; Goodale and Westwood, 2004).

Recently, Valyear et al. (2006) used an event-related fMR-adaptation paradigm to investigate changes in neural activity in the dorsal and ventral streams as a function of object identity and object orientation. Results of this study revealed that a region at the lateral occipito-parietal junction (lOPJ, within the early dorsal stream) showed a selective increase in activity with changes in object orientation, but was insensitive to changes in object identity. In contrast, a region in the occipito-temporal (OT) cortex (within the ventral stream) showed selective increases in activity with changes in identity but was insensitive to changes in orientation. In the context of the Milner and Goodale (1995) model, the authors argued that OT cortex, as a part of the ventral stream, should be sensitive to changes in identity, but not orientation, since the role of this stream is to enable object recognition whatever the observer's viewpoint. In contrast, they proposed that lOPJ, as part of the dorsal stream, should be sensitive to orientation changes, since these would modulate the mechanics of

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actions made toward an object, but not identity changes, as long as these would not affect the parameters of the movements made. For example, very different wrist and hand movements would be required to pick up a hammer disposed in one orientation compared to an orientation at right angles to it; but the actions for picking up a hammer and a knife may be similar if the two target objects share the same orientation. According to this interpretation, however, the effects described by Valyear et al. (2006) should be most clearly observed when the pictures presented to subjects were of real-world graspable objects, such as tools. It is unclear from their data whether this is so because all of the stimuli used in their experiment were graspable objects. Yet this seems important to establish, since if the same orientation selectivity is present also for non-graspable objects, then Valyear et al.'s (2006) interpretation would lose its plausibility.

Although the task used by Valyear et al. (2006) did not explicitly require any visuomotor processing per se, converging evidence suggests that when viewing a tool or graspable object, action-related information is automatically invoked. For example, it has been shown that the position of an object's handle has a significant effect on speed of key press response (e.g. handle orientation towards the right facilitates key presses with the right hand), despite the fact that the position of the handle was irrelevant to the task (Tucker and Ellis, 1998). In addition, single-unit recording studies with monkeys have shown that a subpopulation of grasp-related neurons in area AIP discharge when the monkey views a preferred graspable object, even when no action is required (Sakata et al., 1995; Murata et al., 1997). Studies such as these suggest that simply viewing a graspable object causes action-related information to be automatically represented.

Recent fMRI evidence also suggests that areas within the human dorsal stream can be recruited by the presentation of manipulable objects, even in the absence of an explicit action. It has been found that viewing and naming tools (compared to animals) selectively activated the left ventral premotor cortex (BA 6) (Chao and Martin, 2000), an area which has been activated in PET studies of imagined hand movements (Decety et al., 1994; Stephan et al., 1995; Grafton et al., 1996) and is a possible human homologue of monkey premotor area F5, which forms part of the grasping circuit with area AIP. In addition, they found activity in the left posterior parietal cortex, in an area close to the anterior part of the intraparietal sulcus that has been identified in fMRI studies of grasping as the likely human homologue of monkey AIP (Binkofski et al., 1999; Culham et al., 2003; Frey et al., 2005). The authors suggested that this area may be related to retrieval of information about hand and finger movements associated with the use of graspable man-made objects. Subsequently, Creem-Regehr and Lee (2005) carried out an fMRI experiment in which participants were presented with images of tools with familiar functional identity (such as a hammer, scissors or a hairbrush) or neutral shapes (such as a block, a cylinder or a cone) and were asked to either passively view or imagine grasping them. Passive viewing of tools (vs. scrambled tools) produced activation in the ventral premotor area and posterior parietal cortex, but passive viewing of shapes (vs. scrambled shapes) did not. During imagined grasping, dorsal stream activation in parietal and frontal cortex was observed for both tools and shapes; however, there was still greater activation of the premotor and parietal cortex (as well as other areas) for tools as compared with shapes. Their results suggest that objects that have an associated function produce greater activation than neutral objects and support the suggestion that tools invoke motor representations even during passive viewing.

The aim of the present experiment was to determine whether dorsal stream selectivity to orientation changes is specific to graspable objects. Participants viewed sequential pairs of graspable real world objects (i.e. tools and kitchen utensils) and non-graspable real world objects (i.e. furniture and vehicles). In half the trials, the second item in the pair had the same orientation as the first; in the other half, the orientation changed such that the object was flipped 180° on its horizontal axis. For graspable objects, the 180° flip would alter the way in which one would be required to pick the object up because leftward or rightward direction of the handle would reverse. If, as Valyear et al. (2006) proposed, areas within the dorsal stream are orientation-selective because orientation affects the motor affordances of objects, then we predict that orientation selectivity in the dorsal stream will be limited to objects which can be acted upon as wholes, that is, graspable objects. Alternatively, if the area is selective for changes in orientation in general, comparable orientation selectivity should be observed for both graspable and non-graspable objects. It should be noted that in the study of Valyear et al. (2006), the orientation changed by 90°, whereas here they changed by 180°. Although both orientation changes would affect the motor affordances considerably, the 180° shift keeps the principal axis the same (horizontal), reducing the likelihood that any orientation-selective responses are due to low-level orientation features.

Materials and methods

Participants

Ten neurologically healthy participants took part in the study, 6 male and 4 female, age range 23–40 years old. All subjects were right-handed by self-report and had normal or corrected-to-normal vision. Each participant provided informed consent according to procedures approved by the University of Western Ontario Review Board for Health Sciences Research Involving Human Subjects.

Stimuli

The visual stimuli were presented to the participants using a video projector which was connected to a PC. The images were rear-projected onto a screen which straddled the participant's waist while they lay supine in the scanner. A small mirror was attached to the head coil and was tilted to allow participants to view the stimuli on the screen.

One hundred stimuli were selected from the Hemera Photo-Objects image database. Stimuli were two-dimensional photographs of either graspable objects (50 stimuli) (i.e. tools or household utensils) or non-graspable objects (50 stimuli) (i.e. vehicles or furniture). All images selected had a horizontal principal axis. Images were then rendered in grayscale and resized (to 320×320 pixels) using Adobe Photoshop. Each of the images was flipped 180° along the horizontal axis for use in the orientation change condition. A mask stimulus was created by using *Matlab* (MathWorks, Inc.) to divide an image into a grid of 10×10 cells (each comprising 32×32 pixels), which were randomly reordered. A fixation cross was superimposed in the middle of each image. Stimuli were presented using Super Lab (Cedrus Corp., San Pedro, California).

Procedure

Each event-related experimental run was 6 min 43.5 s in length (269 volumes of 1.5 s each) and participants underwent between 5 and 10 experimental runs (depending on time constraints). Each run comprised 20 stimulus events, which were separated from each other by a fixation period presented for a duration of 12, 13.5 or

15 s (chosen at random). This was long enough to allow the BOLD signal to return to baseline level before the next stimulus was presented. Each stimulus event consisted of a prime stimulus (1.5 s), followed by a mask (1.5 s), followed by a target stimulus (1.5 s) and ending with a mask (1.5 s), for a total event duration of 6 s. The prime stimulus was a graspable or non-graspable image and the target stimulus was always the same object as the prime; however, the orientation of the target stimulus could either be the same or different (flipped along the horizontal axis). Accordingly there were a total of four event types: (1) graspable object, orientation same (G-OS); (2) graspable object, orientation different (G-OD); (3) non-graspable object, orientation same (NG-OS); (4) non-graspable object, orientation different (NG-OD) (see Fig. 1). Each event type occurred randomly five times during each run, and a total of 20 different object identities were used during each run (i.e. each trial used a different object identity). To minimize intertrial adaptation, each stimulus only appeared once within five possible orders for runs. In some subjects who performed more than five runs, orders were repeated. For graspable objects, the handle was on the left in half the trials and on the right in the other half; for non-graspable objects, the front of the object was on the left in half the trials and the right in the other half. Participants were instructed to fixate centrally throughout each event. They were told that they would see two sequential masked stimuli in each trial and their task was to decide if the orientation of the two stimuli was different (as indicated by pressing one key on the response box) or the same (as indicated by pressing an alternate key on the response box). The perceptual task was used because attention to a dimension of interest increases fMR adaptation effects (Murray and Wojciulik, 2004).

Imaging parameters

We used a 4-T, whole-body Varian-Siemens MRI system (Palo Alto, California; Erlangen, Germany) and a quadrature radio-frequency head coil, located at the Robarts Research Institute (London, ON, Canada). Each imaging session consisted of both functional scans and a high resolution anatomical scan. Functional volumes were collected every 1.5 s using a T2*-weighted, segmented (navigator-corrected), interleaved spiral acquisition (2 segments/plane, each with repetition time (TR) = 750 ms for a total volume acquisition time of 1.5 s; time to echo (TE) = 15 ms; flip angle = 45°) for blood oxygenation level-dependent (BOLD) imaging (Ogawa et al., 1992). A single volume covered 14 continuous, 6 mm, pseudo-axial slices, ranging from the most superior point of the cortex down through the ventral fusiform cortex. The imaging field of view was 22 cm × 22 cm, for a voxel resolution of 3.4 mm × 3.4 mm × 6 mm. High resolution T1-weighted anatomical volumes were acquired using 3D magnetization-prepared FLASH acquisition (T1 = 1300 ms, TE = 3 ms, TR = 50 ms, FA = 20°).

Analysis

The imaging data were pre-processed and analyzed using Brain Voyager QX (Brain Innovation, Maastricht, Netherlands). Anatomical volumes were transformed into a brain space that was common for all participants (Talairach and Tournoux, 1988). Each functional run was screened for head movements using Brain Voyager 3D motion correction parameter plots and those that were found to be significantly corrupted (i.e. containing abrupt or cumulative movements greater than 1 mm or 1°) were removed from the analysis. Each run underwent temporal high-pass frequency filtering to remove low frequency trends (below 2 cycles per scan). Functional volumes were then aligned to the transformed anatomical volumes, so that all functional data were transformed into a standard stereotaxic space (Talairach and Tournoux, 1988).

The data were analyzed using a general linear model (GLM) in Brain Voyager QX. Random effects analyses were performed to ensure that effects could not have been driven by only a small number of participants and that the results were applicable to the general population. Two main statistical contrasts were performed by contrasting the orientation different from the orientation same trials for: (1) graspable objects (G-OD versus G-OS); (2) non-graspable objects (NG-OD versus NG-OS). Thus, orientation sensitivity was assessed independently for each of the two stimulus categories. Resultant activation maps were set to a minimum cluster size threshold (k) of 100 mm^3 and a minimum significance threshold of $t = 3.80$. These minimum statistical settings were determined by a data-driven approach to ensure that there were no false-positive activations in another contrast for which no significant differences would be expected. That is, we first pseudo-randomly divided the trials into four arbitrary sets, each with an equivalent number of events from each of the four original conditions. In principle, contrasting any two of these conditions should not yield any legitimately active clusters; thus, falsely activated clusters would suggest an overly liberal threshold. We performed contrasts between each possible pair of conditions against the remaining pair and adjusted the threshold and cluster size until no significant clusters were found. At the above thresholds ($k = 100$ mm^3, $t = 3.8$) no voxels were found to be significantly active in these arbitrary contrasts. This combination of threshold and cluster size was also found to be acceptable through Monte Carlo simulations of data sets of the same size (AlphaSim, Douglas Ward); however, we believe the slightly more conservative levels we determined through our approach are better because they are based on real data and do not make assumptions about the statistical independence of adjacent voxels.

Once the orientation-sensitive areas were identified for each of the stimulus categories, averaged time courses were extracted from the regions and converted into percent signal change. Various planned comparisons were then conducted on the data. These included, determining main effects of orientation (G-OD and NG-OD versus G-OS and NG-OS) and category (G-OD and G-OS versus NG-OD and NG-OS), and also contrasting orientation-different versus orientation-same trials for both the graspable (G-OD versus G-OS) and non-graspable (NG-OD versus NG-OS) categories of objects. This analysis was carried out to determine if regions identified in the main contrasts were selective for one of the categories of objects or whether they were selective for orientation *per se*.

Results

To identify regions that were sensitive to changes in the orientation of graspable objects, we contrasted activation in the G-OD vs. G-OS conditions. To ensure that this activity would also be greater than the intertrial baseline, we added a contrast of the G-OD condition versus the intertrial fixation baseline [that is, we performed a conjunction between (G-OD vs. G-OS) AND (G-OD vs. baseline)]. This revealed one significant cluster of activation: in

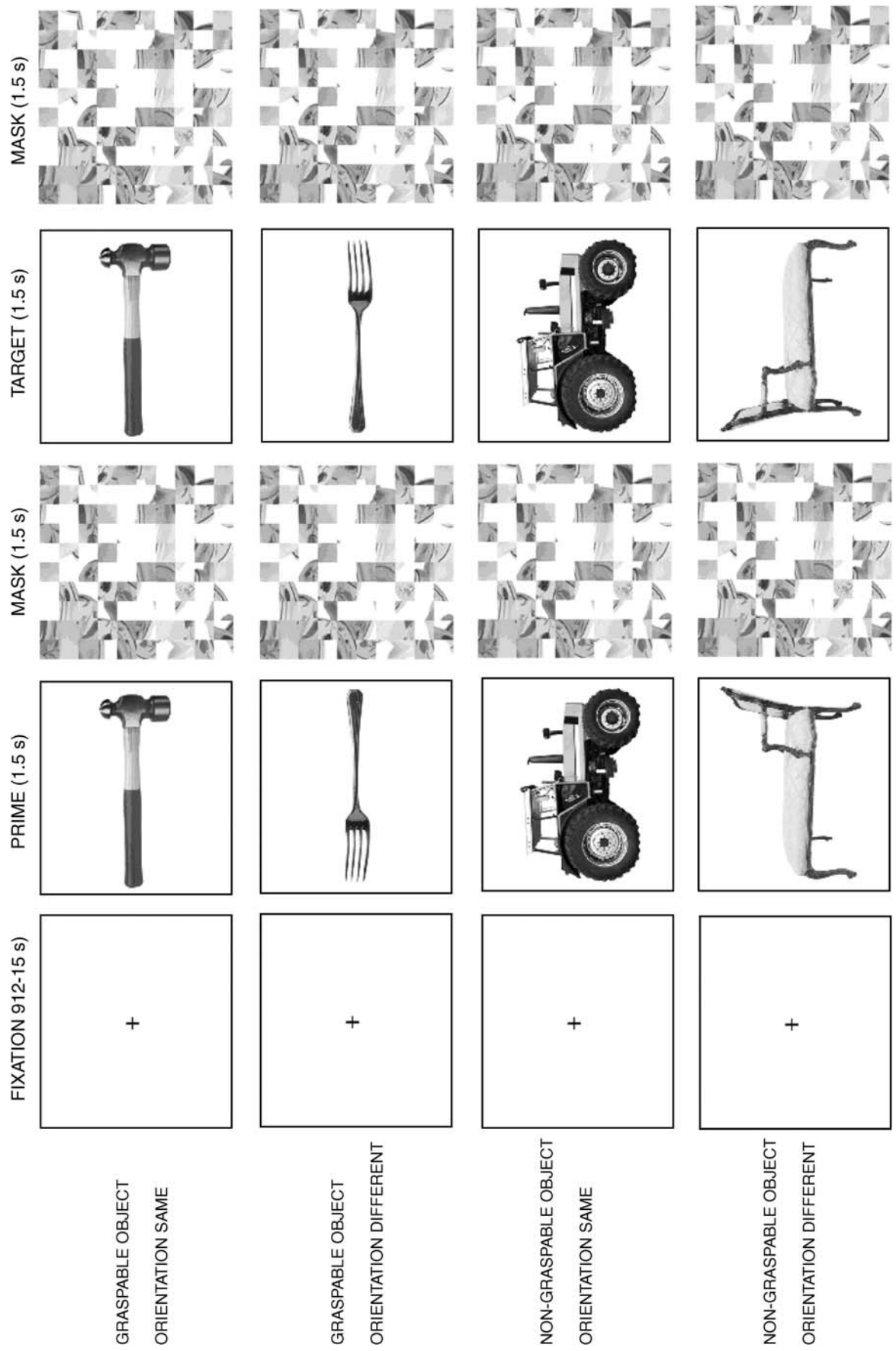

Fig. 1. Stimuli and timing for each of the four event types.

the right hemisphere at the lateral occipito-parietal junction (lOPJ) (Figs. 2a and b). To identify regions that were sensitive to changes in the orientation of the non-graspable objects, a contrast was made between the averaged BOLD response associated with the NG-OD condition against the averaged BOLD response associated with the NG-OS condition. Again, to ensure that this activity was greater than baseline a conjunction comparison was added contrasting the NG-OD condition versus the baseline [(NG-OD vs. NG-OS) AND (NG-OD vs. baseline)]. This second contrast revealed no significant clusters of activation.

The cluster of activation which demonstrated orientation selectivity for graspable objects (in right lOPJ) did not demonstrate significant orientation selectivity for non-graspable objects. Specifically, the planned comparison between orientation change and no change was significant for the graspable objects (G-OD vs. G-OS, $t=4.764$, $p=0.001$), but not for the non-graspable objects (NG-OD vs. NG-OS, $t=0.807$, $p=0.440$). There was a significant main effect of orientation ($t=2.266$, $p=0.05$) and a significant main effect of category ($t=6.726$, $p<0.001$); this reflects higher responses for orientation change conditions and higher responses for graspable objects. The focus of activation we found here (Talairach coordinates: $x=24$, $y=-84$, $z=7$) corresponds remarkably well to the orientation-selective focus in Valyear et al. (2006) ($x=22$, $y=-81$, $z=19$). To further illustrate this finding we computed the adaptation index for both the graspable and non-graspable objects. The adaptation index was calculated using the formula $(OD-OS)/(OD+OS)\times 100\%$ for each stimulus category, such that an index of zero would indicate no adaptation and higher values indicate the size of the adaptation effect as a percentage of the overall response amplitude (relative to the intertrial baseline). As can be seen in Fig. 2c, participants had higher and much more consistent levels of adaptation for the graspable objects than the non-graspable objects.

Discussion

The aim of the present experiment was to determine if selectivity to orientation changes within the dorsal stream is restricted to graspable objects. Participants were presented with an image of either a graspable or non-graspable real object, which was followed by the same image in either the same or different orientation (i.e. flipped on the horizontal axis). A comparison was made between orientation-change and no-change conditions within the graspable object category. This revealed one cluster of activation, in area lOPJ of the right hemisphere, and this area was shown to be sensitive to orientation changes in the graspable object category only. No areas of activation were revealed for a comparison of orientation change versus no change within the non-graspable object category.

We found that the lOPJ in the right hemisphere was orientation-selective, consistent with Valyear et al. (2006), but more importantly, we found that this orientation selectivity was present only when the stimuli were graspable objects. Valyear et al. (2006) suggested that the most likely candidate for a functionally similar region to lOPJ in the macaque is an area in the lateral bank of the caudal intraparietal sulcus (CIP) and further suggested that the human equivalent of CIP might in fact overlap with the area they identify as lOPJ. In the macaque brain, CIP contains neurons that respond selectively to three-dimensional (3D) features of an object, such as shape and orientation (Sakata et al., 1998; Taira et al., 2000; Tsutsui et al., 2002). This area not only contains neurons tuned to object orientation but sends projections to the anterior intraparietal area (AIP) for the visual guidance of hand actions (Sakata et al., 1997, 1999). Human imaging studies have suggested there is a region in the caudal part of the intraparietal sulcus in the human brain which becomes active during object matching and grasping and during discrimination of object size and orientation (Faillenot et al., 1997, 1999). In another study, it was proposed that a possible human equivalent of monkey CIP exists in the posterior part of the intraparietal sulcus bilaterally (Shikata et al., 2003). This region was activated by a comparison between orientation and color discrimination tasks, and the authors suggested that human CIP, like macaque CIP, is involved in coding the 3D features of objects. It is thus possible that the region in the lOPJ of the right hemisphere observed in the present study codes the orientation of objects to be grasped, providing an input into the human equivalent

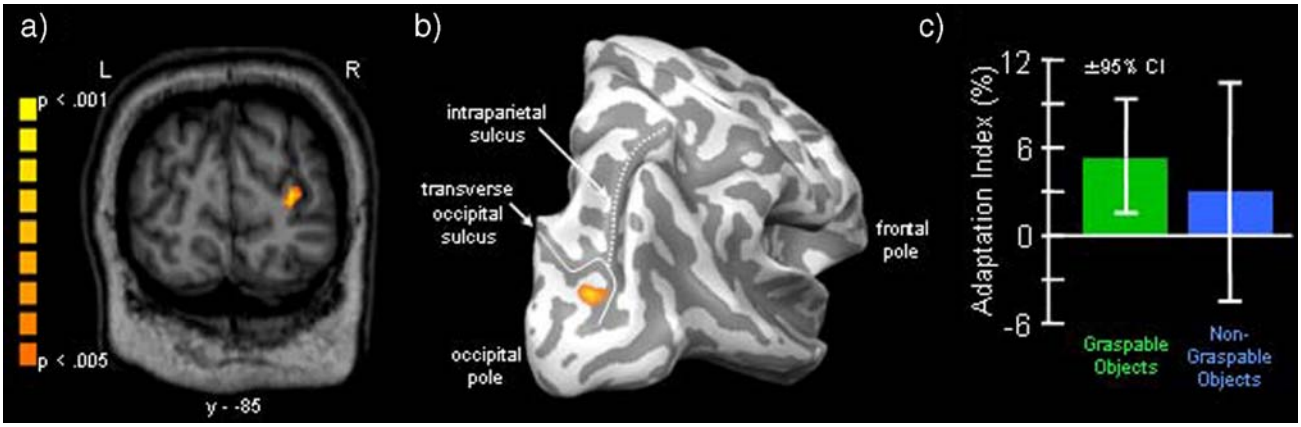

Fig. 2. (a) The activation identified by contrasting orientation different versus orientation same within the graspable object category. The area defined lies at the lateral occipito-parietal junction on the right hemisphere. Talairach coordinates: $x=24$, $y=-85$, $z=6$; cluster size=132 mm^3. (b) Postero-lateral view of the partially inflated right hemisphere of a representative subject illustrating the location of the lateral occipito-parietal junction activation. Concavities (sulci) are dark gray; convexities (gyri) are light gray. (c) Bar graph illustrating average adaptation index, with 95% confidence intervals. The adaptation index for each category was computed according to the following formula: $(OD-OS)/(OD+OS)\times 100\%$. Note that an index of zero would indicate no adaptation and the confidence intervals for the non-graspable objects include zero.

of AIP (Binkofski et al., 1999; Culham et al., 2003; Frey et al., 2005), which has recently been demonstrated to be involved in the execution of a grasping movement (Rice et al., 2006b).

Given that our subjects were right-handed, one may have expected more activation in dorsal stream areas in the left hemisphere, rather than the right hemisphere as we observed; however, data from past studies have been mixed with respect to the laterality of this area. For example, Valyear et al. (2006) also reported activation only in the right lOPJ. Similarly, Faillenot and colleagues (1999) revealed activation in the posterior part of the intraparietal sulcus in the right hemisphere in an orientation discrimination task. It has also been suggested that the perception of structure based on shading revealed activation in the caudal part of the intraparietal sulcus in the right hemisphere (Taira et al., 2001). In a later study however, it was shown that activation in the caudal part of the intraparietal sulcus of the left hemisphere (Faillenot et al., 2001). Finally, studies have shown activation bilaterally in the posterior portion of the intraparietal sulcus for orientation discrimination (Shikata et al., 2001, 2003). While the evidence of hemispheric lateralization is equivocal, Shikata et al. (2003) argue that the right parietal cortex is more involved in visuospatial information processing, whereas the left is more involved in visuomotor integration. Therefore, it is possible that the task employed (i.e. to detect a change in orientation) can account for this, as this is predominantly a visuospatial task.

One other explanation for the observed results being lateralized to the right hemisphere could be due to a role of spatial attention, for example if subjects attend to a particular aspect of the stimulus and wait to see if a change occurs within the attended portion of the stimulus. Such an explanation would be supported by findings illustrating a role of the right hemisphere in spatial attention, for example Foxe and colleagues (2003) have shown that an area in the right parieto-occipital cortex (an area in close proximity to the area we identify in the present experiment) is involved in line bisection judgments (a task which involves voluntary orienting of spatial attention to an object) (Foxe et al., 2003). We do however feel that such an explanation is unlikely for several reasons. Firstly, if orientation changes caused an increase in spatial attention one would expect to see an increase in neuronal activity for orientation shifts of both graspable and non-graspable objects. Secondly, in the study by Valyear et al. (2006) subjects were passively viewing the stimuli, yet the same pattern of activation was observed for orientation changes. Finally, previous imaging studies have identified area LIP as being responsive during saccadic eye movements and shifts in spatial attention (Corbetta et al., 1998; Beauchamp et al., 2001), yet no differential LIP activation was observed in the present study.

Surprisingly, although lOPJ only demonstrated orientation selectivity for graspable but not non-graspable objects, it was overall more activated by non-graspable objects (see Fig. 2). Two explanations are possible. First, the non-graspable stimuli tended to have a larger retinal image size and to be less elongated than the tools; for example, in Fig. 1 the tractor and lounge chair are taller than the hammer and fork. Thus, it is possible that lOPJ would be driven more strongly by non-graspable objects if it was sensitive to object size (and perhaps object features). A second possibility is that the non-graspable stimuli represented objects that were much larger in the real world than the graspable stimuli and would typically be processed in peripheral vision. Recent evidence has suggested that areas within both the dorsal and ventral streams show preferred responses to objects typically associated with processing in particular parts of the retina (Malach et al., 2002; Hasson et al., 2003). For example, within the ventral stream, the fusiform face area demonstrates a preference for faces (vs. places or objects) and for stimuli in central (vs. peripheral) vision, presumably because faces are typically seen in the fovea; whereas, the parahippocampal place area demonstrates a preference for places (vs. faces and objects) and for stimuli in peripheral vision, presumably because places are typically processed in peripheral vision (Levy et al., 2001). Although this eccentricity-based organizational principle has not received as much attention in dorsal as in ventral stream areas (Hasson et al., 2003) have observed a preference for peripheral stimuli (namely buildings over objects and faces) around the lOPJ bilaterally, near the junction of the intraparietal and transverse occipital sulci (±33, 78, 12), quite close to the lOPJ focus we have reported here. Thus, one possible explanation would be that lOPJ is involved in processing visual information for action with an emphasis on peripheral vision, where actions typically take place. The peripheral preference could thus lead to a stronger response to the non-graspable stimuli, although the processing for action would lead to orientation selectivity only for graspable objects. Regardless of the explanation for the differential category activation in lOPJ, our primary interest is in the orientation selectivity. In complex areas with heterogeneous populations of neurons, the power of the fMR adaptation technique lies in its ability to reveal selectivity rather than just overall activation levels.

There were some differences between the present study and the design employed by Valyear et al. (2006), which should be noted. First, in the present study the orientation change was a flip on the horizontal axis, allowing the principal axis to remain unchanged. In contrast, Valyear et al. (2006) used stimuli which were tilted either 45° to the left or right of the horizontal meridian with respect to the observer. One other difference between the two experiments is that the present study employed a task where participants were required to attend to the orientation of the stimuli. Yet despite the differences in the two experiments the same region in the lOPJ was shown to be sensitive to orientation changes of graspable stimuli.

In conclusion, the present study provides evidence to suggest that the dorsal stream's sensitivity to orientation changes, previously observed in area lOPJ in the right hemisphere (Valyear et al., 2006), is specific to graspable objects only, presumably because such changes would affect the way in which an object would be grasped. This area is possibly functionally equivalent to area CIP in the macaque brain which has been shown to be sensitive to the 3D features of an object and which sends projections to AIP for guiding grasping.

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