



Parietal and frontal object areas underlie perception of object orientation in depth

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ABSTRACT

Recent studies have shown that the human parietal and frontal cortices are involved in object image perception. We hypothesized that the parietal/frontal object areas play a role in differentiating the orientations (i.e., views) of an object. By using functional magnetic resonance imaging, we compared brain activations while human observers differentiated between two object images in depth-orientation (orientation task) and activations while they differentiated the images in object identity (identity task). The left intraparietal area, right angular gyrus, and right inferior frontal areas were activated more for the orientation task than for the identity task. The occipitotemporal object areas, however, were activated equally for the two tasks. No region showed greater activation for the identity task. These results suggested that the parietal/frontal object areas encode view-dependent visual features and underlie object orientation perception.

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The neural basis for object perception has been attributed to the lateral and ventral surfaces of the occipital and temporal cortices [11,20]. Those regions, including the lateral occipital area, fusiform gyrus (FuG), and inferior temporal gyrus (ITG), are often referred to as the lateral occipital complex (LOC) [11]. However, object-related responses have also been found in the parietal and frontal cortices. The LOC and regions around the intraparietal sulcus (IPS) often show larger activations for object images than for non-object images [17,23]. The inferior frontal cortex (IFC) is object-sensitive as well [2,23,24].

What is the functional role of the parietal/frontal areas in object perception? Although it is well known that the dorsal visual system controls visual attention that selects objects [5], ample evidence suggests that the parietal/frontal areas may underlie more detailed analysis on object images after attentional selection.

First, electrophysiology of the macaque monkey brain and human imaging studies have shown that the monkey/human IPS is sensitive to 3D spatial features (shape, orientation) of objects [8,21,26] that may be useful for visually guided, object-

directed actions. In addition, imaging studies implied that the frontal/parietal responses to object image stimuli are related to action [4,18,30]. These studies suggested that the parietal/frontal object areas might encode visual features required for grasping or manipulating objects (e.g., affordance).

Meanwhile, without explicit relations to action, the parietal/frontal areas still have functional roles in object image perception, including: mental rotation, perception of accidental (non-canonical and unfamiliar) views, and object-orientation judgment. The mental rotation task of either 3D or 2D objects recruits the superior parietal lobule (SPL), IPS, areas around the precentral sulcus, and the ventral prefrontal cortex (PFC) [33]. Lesions including the right parietal cortex often impaired visual recognition of objects in accidental views [16,32] and orientation judgment of objects (object orientation agnosia) [14,28]. Imaging studies [19,25,27] also suggested the involvement of the parietal/frontal regions in viewing or naming accidental-view objects. The contribution of the parietal areas to the perception of object orientation in the picture plane (e.g., upright, rotated clockwise, etc.) was also suggested [15]. It has been suggested that the parieto-occipital areas are sensitive to object orientation changes in the picture plane, while the ventral occipitotemporal areas are sensitive to object identity changes [29].

However, Altmann and colleagues [1] reported that virtually all the object-sensitive areas, including the ventral occipitotemporal area, IPS, and postcentral sulcus, were activated more for object-orientation judgments than for identity judgments, suggesting no difference between the parietal and ventral areas in

Abbreviations: AnG, angular gyrus; fMRI, functional magnetic resonance imaging; FuG, fusiform gyrus; IFC, inferior frontal cortex; IFG, inferior frontal gyrus; IPS, intraparietal sulcus; ITG, inferior temporal gyrus; LOC, lateral occipital complex; MFG, middle frontal gyrus; PCG, precentral gyrus; PCu, precuneus; PFC, prefrontal cortex; SMA, supplementary motor area; SPL, superior parietal lobule.

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object-orientation judgment. This finding seems inconsistent with the implications reviewed above. The discrepancy may be due to the orientations adopted in the study [1]: 0° (upright), 90°, 180° (inverted), and 270°. Objects in the latter three orientations were highly accidental (e.g., inverted bicycle); therefore, they might activate the parietal regions that are sensitive to accidental views irrespective of the task required. It is also likely that the participants performed mental rotation to verify the identities of the rotated object image stimuli, which in turn activated the frontal and parietal object areas for the identity task.

What is the essential information processed by the parietal/frontal object areas? We hypothesized that the critical component common to the previous findings reviewed above is visual differentiation of the orientation/view of the object. Studies using functional magnetic resonance imaging (fMRI) priming techniques [17,31] showed that the parietal regions were sensitive to view changes in 3D objects. Hence, it seems plausible that the parietal object regions play a role in the perception of object orientation in depth by differentiating the view of an object in a given orientation from the view of that object in another orientation, whereas the primary function of the LOC is to integrate the views of various orientations into a single object representation of its identity (i.e., object constancy against viewpoint variation). Note that the object orientation perception may contribute to object-directed hand action, mental rotation, and recognition of an object in accidental view (i.e., accidental orientation). If this was the case, the parietal/frontal areas would be more activated by performing a task to judge object orientation in depth, even when neither mental rotation nor object-directed action was required.

In the present study, we examined the involvement of the parietal/frontal cortices in the visual perception of object orientation in depth (not in the picture plane). Here, we referred to the rotation angle around the vertical axis (i.e., azimuth angle) as orientation in depth. Our participants observed two sequential object images and detected changes either in orientation (orientation task) or in identity (identity task). By using fMRI, we compared the activities observed in the two tasks and examined whether the judgments of object orientation in depth involved the parietal and frontal object areas.

Sixteen neurologically healthy individuals participated (mean age 21.9) in this study. All were right-handed and had normal or corrected-to-normal vision. Each provided written informed consent in advance. The experimental procedure was approved by the ethical committee of Teikyo University.

Each participant performed two tasks in the scanner. In the orientation task, they observed a succession of two object images and judged whether there was an orientation difference. In the identity task, they judged whether there was an identity difference. We manipulated orientation difference and identity difference, yielding four conditions (Fig. 1). Note that in both tasks all of the conditions were used and that participants were instructed to ignore the identity differences in the orientation task and vice versa. The object image pairs used were common to the two tasks.

Object orientations were manipulated by rotating the objects around the vertical axis. One of the paired successive stimuli was presented in one of the standard orientations of 45°, 135°, 225°, and 315° (0° = front). In the same-orientation condition, another object was presented in the same orientation (i.e., 0° difference). In the different-orientation condition, another object was rotated $\pm 15^\circ$ (e.g., 45° was paired with either 30° or 60°). The amount of difference was always 15°. The presentation order of the successive stimuli was randomized. We omitted cardinal orientations such as front and profile because they often yield accidental and unrecognizable views (e.g., a car in front, a laptop computer in profile).

The two successive images depicted identical objects (same-identity condition) or two different identities from the identical

category (different-identity condition, e.g., car A and car B). The category matching in the different-identity condition was intended to roughly equalize the difficulty of the two tasks. We selected 22 categories (i.e., 44 identities) of everyday objects (16 for experimental sessions, 6 for practice sessions) including furniture, vehicles, electronics, animals, etc.

For each task, a single participant performed 64 trials in which the 4 conditions (Fig. 1) equally occurred. The 4 conditions, 16 object categories, and 4 standard orientations yielded 256 trial types; they were performed by every 4 participants so that all of the conditions were equally counterbalanced among the participants.

Object images were generated by 3D graphic software (Shade 6.0, e frontier Inc., Tokyo). The viewpoint was 20° elevated from the horizon. For the control blocks, we used randomly scrambled versions of the object images. All of the stimuli were achromatic. The stimuli were presented as follows. Each trial started with a 200 ms fixation point at the screen center followed by the first stimulus (700 ms). After a 400 ms blank, the second stimulus was presented (700 ms). Participants made responses (button presses for same or different) within a 1000 ms response period with blank display after the stimuli presentations. The next trial immediately followed.

Two functional runs (one for the orientation task and one for the identity task; orders were counterbalanced among participants) and one structural run was conducted for each participant. In between the two functional runs, participants were instructed to switch the task. The experiment was block-designed. Each functional run consisted of 8 task blocks, 8 control blocks, and 8 rest blocks, which were interspersed. In the task block, participants performed either task (orientation or identity) for 8 trials, which contained the four conditions (Fig. 1) equally. Error rates of the button-press responses were recorded as behavioral performances. Reaction times were not recorded. In the control block, they observed passively the scrambled images and pressed either button with no judgment required. During the rest block, they fixated on the continuously blinking fixation point with no response. Each functional run lasted for about 10 min (24 s \times 24 blocks). The four conditions shown in Fig. 1 occurred in equal frequency and in random order. Participants were instructed to focus on the fixation point and the stimuli, though their eye movements were not monitored. Prior to the scans, participants performed brief practice sessions outside the scanner.

Brain activities were measured by using a 1.5-T MRI scanner (Signa LX Scanner, General Electric Medical Systems, Milwaukee, WI). Visual stimuli were presented on a back-projection screen. Stimulus presentation was controlled by Psychophysics Toolbox software [3]. Participants observed the stimuli through a mirror mounted on the MRI head coil.

Functional images were acquired by using T2*-weighted echo planar imaging (TR = 6000 ms, TE = 40 ms, flip angle = 90°, voxel size = 3.75 mm \times 3.75 mm in-plane resolution, slice thickness = 4 mm, 29–31 axial slices covering the whole brain). Prior to the functional scans, high-resolution T1-weighted structural images were acquired and used for anatomical reference (TR = 15 ms, TE = 7 ms, field of view = 24 cm, flip angle = 90°, voxel size = 0.95 mm \times 0.95 mm in-plane resolution, slice thickness = 1.3 mm, 124 axial slices covering the whole brain). The first four images were discarded to allow for stabilization of the magnetization.

Imaging data were analyzed using SPM 5 software [9]. For spatial preprocessing, each participant's scans were realigned to the first volume and then re-sliced and normalized to form a standard template image. The data were smoothed by using an 8 mm full-width at half-maximum isotropic Gaussian kernel. Task and participant effects were estimated according to the general linear model at each voxel in the brain space. We

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