

# Similar cortical correlates underlie visual object identification and orientation judgment

Christian F. Altmann<sup>a,c</sup>, Wolfgang Grodd<sup>b</sup>, Zoe Kourtzi<sup>c</sup>,  
Heinrich H. Bühlhoff<sup>c</sup>, Hans-Otto Karnath<sup>a,\*</sup>

<sup>a</sup> Section Neuropsychology, Department of Cognitive Neurology, Hertie Institute for Clinical Brain Research, University of Tübingen, Tübingen, Germany

<sup>b</sup> Section Experimental MR of the CNS, Department of Neuroradiology, University of Tübingen, Tübingen, Germany

<sup>c</sup> Max Planck Institute for Biological Cybernetics, Tübingen, Germany

Received 9 August 2004; received in revised form 16 March 2005; accepted 17 March 2005

Available online 20 April 2005

## Abstract

Visual object perception has been suggested to follow two different routes in the human brain: a ventral, view-invariant occipital–temporal route processes object identity, whereas a dorsal, view-dependent occipital–parietal route processes spatial properties of an object. Using fMRI, we addressed the question whether these routes are exclusively involved in either object recognition or spatial representation. We presented subjects with images of natural objects and involved them either in object identification or object orientation judgment task. For both tasks, we observed activation in ventro-temporal as well as parietal areas bilaterally, with significantly stronger responses for the orientation judgment in both ventro-temporal as well as parietal areas. Our findings suggest that object identification and orientation judgment do not follow strictly separable cortical pathways, but rather involve both the dorsal and the ventral stream.

© 2005 Elsevier Ltd. All rights reserved.

**Keywords:** Object recognition; Object orientation; View-based; functional MRI; Orientation agnosia; Visual processing

## 1. Introduction

Successful interaction with our environment entails that we are capable of visually recognizing objects from many different viewpoints and judging their position in space. The question of how our brain copes with changes in view, scale, and orientation when recognizing objects has been the subject of many studies from various fields in neuroscience.

One possibility would be that recognizing objects is independent of the orientation of an object. In fact, viewpoint-invariant theories hold that the representations are stored in an object-centered frame of reference based on the objects' geometry, e.g., their principal axes (Marr & Nishihara, 1978) or by orientation-free unique features of the object (Corballis,

1988). Object recognition thus could be achieved without mental transformations to align the respective image of an object with a represented view of it. In contrast, view-based theories of object-recognition postulate that objects are represented by previously seen and stored images of the object. Thus, object recognition requires interpolation between the visual input and the stored view of the object (Bühlhoff & Edelman, 1992; Shepard & Cooper, 1982; Tarr, 1995; Ullman, 1989). Since both views are plausible from a computational perspective and have psychophysical evidence in their favor, the question arises how this is implemented in the human brain.

Early observations in brain-damaged patients were interpreted as evidence that separate cortical centers underlie visual object recognition and processing of spatial features. Best (1917) described a patient that presented with impaired knowledge of object orientation but spared object recognition skills. Similar cases exhibiting this peculiar dissociation have been described since Best's discovery (for review see Ferber

\* Corresponding author. Present address: Center of Neurology, University of Tübingen, Hoppe-Seyler-Str. 3, D-72076 Tübingen, Germany. Tel.: +49 7071 2980465; fax: +49 7071 295957.

E-mail address: Karnath@uni-tuebingen.de (H.-O. Karnath).

& Karnath, 2003). One study even described a double dissociation between object identification and orientation (Turnbull, 1997). These observations have been taken as evidence for two routes in the visual system: an orientation-dependent and an orientation-invariant route for object recognition. This is in line with the model of Ungerleider and Mishkin (1982) that describes a ventral path for visual recognition and a dorsal path for processing of spatial object attributes. However, recent studies described patients with spared object recognition and deficits of object orientation perception when objects were in non-upright positions only (Harris, Harris, & Caine, 2001; Karnath, Ferber, & Bühlhoff, 2000). That is, knowledge of object orientation was impaired only in non-canonical views, while perception of the upright position was preserved. This suggests that the cortical substrates that underlie object recognition and orientation judgment are not entirely separable. It might be that lesions that provoke orientation agnosia affect a general object recognition network and harms the most vulnerable parts first, that is the processing of orientation of objects that are seen from non-canonical views.

Functional magnetic resonance imaging (fMRI) as a non-invasive method has been used to investigate the neural mechanisms that underlie object recognition and spatial processing. So far, different – in part even contradictory – observations have been reported. On the one hand, ventro-temporal object-selective areas have been shown to be invariant to changes in viewpoint (James, Humphrey, Gati, Menon, & Goodale, 2002), while parietal areas encode objects in a view-dependent manner. In contrast, previous fMRI adaptation studies reported view-dependency in lateral occipital areas and in posterior fusiform gyrus (Grill-Spector, Kushnir, Edelman, Avidan, Itzhak, & Malach, 1999). To complicate the picture, a recent fMRI priming study revealed hemispheric lateralization of viewpoint-dependency, that is view-invariance in the left fusiform gyrus, while the right fusiform gyrus was involved in a view-dependent representation of objects (Vuilleumier, Henson, Driver, & Dolan, 2002). James et al. (2002) argued that the different results observed in these studies might be accounted for by differences in stimulus timing, the extent of the rotation, the extent of the region of interest under investigation and the subjects' task. A recent study observed a dissociation of viewpoint-dependency in the superior parietal lobe and the fusiform gyrus during mental rotation and object recognition (Gauthier, Hayward, Tarr, Anderson, Skudlarski, & Gore, 2002). Particularly, the superior parietal lobe showed viewpoint-dependent involvement in object representation preferentially during the mental rotation task, while the fusiform gyrus showed viewpoint-dependency during object recognition. The results further suggested a dorsal–ventral dissociation, that is recruitment of dorsal areas during mental rotation and of ventral areas during object recognition. In contrast, previous brain imaging studies also provide evidence that ventro-temporal and parietal cortical areas are involved in both object recognition and spatial processing tasks, namely processing of location

and mental rotation (Faillenot, Toni, Decety, Gregoire, & Jeannerod, 1997; Marois, Leung, & Gore, 2000; Vanrie, Beatse, Wagemans, Sunaert, & Van Hecke, 2002).

In the present study, we addressed the question whether visual object identification and object orientation perception involve different cortical areas or share common neural substrates. We presented subjects with images of real-world objects and involved them either in an object identity matching task or an object orientation matching task. The aim of this experimental manipulation was to provide evidence to either corroborate or falsify the assumption of a double-dissociation between object identification and orientation judgment capabilities in healthy subjects.

## 2. Methods

### 2.1. Subjects

Fifteen right-handed students (aged 19–36) from the University of Tübingen participated in a first experiment (Experiment 1). A subset of 10 subjects also participated in a second experiment (Experiment 2) in the same session. All subjects had normal or corrected to normal visual acuity and gave their informed consent to participate in the study, which was performed in accordance with the ethical standards laid down in the 1964 declaration of Helsinki.

### 2.2. Stimuli

In our study, we used 40 images, which included both animals and man-made objects, provided courtesy of Michael J. Tarr (Brown University, Providence, RI). The stimuli were presented under Matlab, using the Psychophysics Toolbox extensions (Brainard, 1997). The images were presented in three different colors (red, green, and blue) and exhibited four different rotations in the picture plane, namely 0°, 90°, 180°, and 270° (Fig. 1). The size of the whole display was 9.5° of visual angle. The same stimuli were presented in all experimental conditions.

### 2.3. Procedure

The two experiments consisted of five different conditions: “Fixation”, “Object Identification”, “Orientation Judgment”, and control conditions for the Object Identification and for the Orientation Judgment task.

In the fixation block, the subject was first presented with a 3 s instruction “Fixate”, followed by a central fixation dot, shown for 18 s. In the experimental conditions, subjects were first presented with the instructions “Same Object”, “Same Orientation” or “Same Color”, followed by a 24 s block in which they had to perform eight trials of the announced matching task. Each 24 s block consisted of eight 3 s trials in which the first image was presented for 300 ms, followed by a 400 ms inter-stimulus blank and a 300 ms presentation

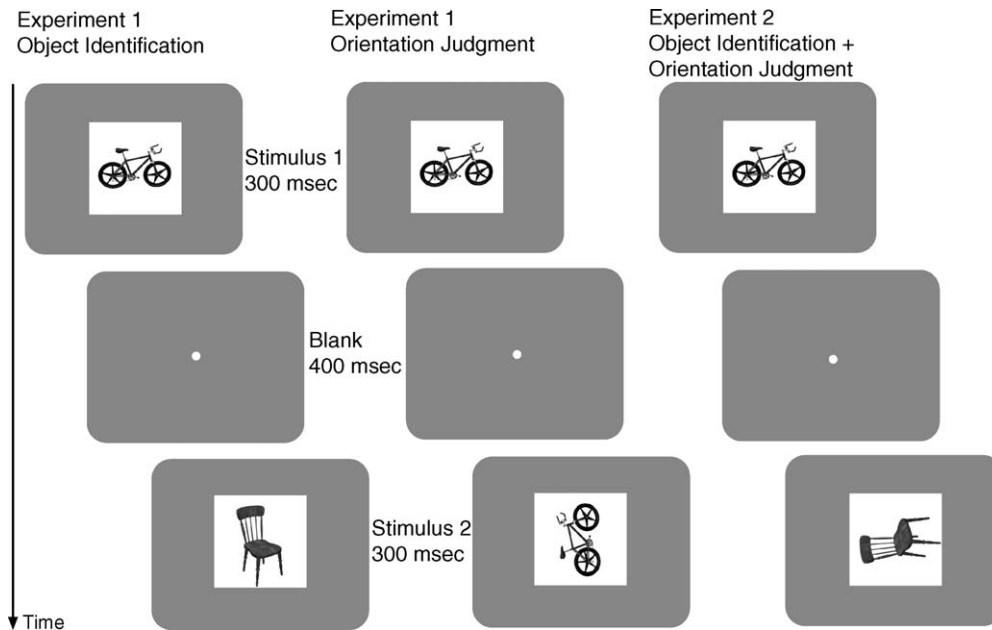


Fig. 1. Sample trial sequences used in Experiment 1 (left and middle column) and Experiment 2 (right column). The images were presented in one of three colors (red, green, blue) in all conditions. For Experiment 1, the images were presented upright in the Object Identification blocks and subjects were instructed to match the identity of the objects (left column). In the Orientation Judgment blocks in Experiment 1, the images were presented in one of four orientations ( $0^\circ$ ,  $90^\circ$ ,  $180^\circ$ , or  $270^\circ$ ) and subjects were instructed to match the orientations of two identical objects (middle column). In Experiment 2, in both the Object Identification and the Orientation Judgment blocks, images were presented in one of four orientations ( $0^\circ$ ,  $90^\circ$ ,  $180^\circ$ , or  $270^\circ$ ) with same or different objects in both conditions (right column).

of the second image. Between trials, a blank was presented for 2 s.

In Experiment 1, during the Object Identification task (“Same Object”), the two images were presented upright and subjects had to match their identity by pressing one button for same and another button for different objects. In the Orientation Judgment task (“Same Orientation”), two images of the same object were presented in one of four orientations ( $0^\circ$ ,  $90^\circ$ ,  $180^\circ$ , and  $270^\circ$ ) and subjects were instructed to match the orientation of the two objects. Finally, in the color control tasks (“Same Color”), stimulation within a block was similar to either the Object Identification or the Orientation Judgment block, but subjects had to perform a color matching task, regardless of object identity or orientation. In all the experimental blocks half of the trials were match trials and half non-match trials.

To avoid that differences between conditions can be accounted for by differences in stimulation or task difficulty, we conducted a second experiment (Experiment 2) in the same session. This control experiment employed the same stimuli, tasks and procedure as Experiment 1. The only difference was that visual stimulation was identical during all tasks. More specifically, in the Object Identification task, same or different objects were presented at same or different orientations and colors. In the Orientation Judgment and the Color Matching tasks, the same stimulus set was shown. This required subjects to match object identity between rotated objects and to match orientation across different objects.

Subjects were administered four runs of stimulus presentation in Experiment 1, as well as a high-resolution T1-weighted MPRAGE sequence. Subjects that also underwent Experiment 2 were administered four additional runs. The order of the experiments was counterbalanced across subjects. Visual stimuli were presented with an LCD projector, mirrored towards the subject’s eye. Each experimental run took 7 min and 15 s and consisted of four 24 s epochs for both the Object Identification and Orientation Judgment conditions, and two 24 s epochs for each of the color control conditions. In addition, four 18 s fixation epochs were shown. Before each epoch, a 3 s instruction was presented. The order of the experimental epochs was randomized for each subject and each run, to balance for order effects.

#### 2.4. *Imaging and data analysis*

All imaging was conducted on a 1.5 T Siemens Sonata scanner at the University Clinic in Tübingen, Germany. An echo planar imaging sequence with gradient echo sampling ( $TR=3$  s,  $TE=40$  ms) was used to acquire the functional imaging data. Thirty axial slices (5 mm thick with  $3.00$  mm  $\times$   $3.00$  mm in-plane resolution), covering the whole brain, were collected with a head coil. The field of view was  $19.2$  cm  $\times$   $19.2$  cm with an in-plane resolution of  $64$  pixel  $\times$   $64$  pixel.

fMRI data were processed using the BrainVoyager<sup>TM</sup> 4.9 software package. Preprocessing of functional data included slice scan time correction, head movement correction and

removal of linear trends. The 2D functional images were aligned to 3D anatomical data, transformed to Talairach & Tournoux standard coordinates (Talairach & Tournoux, 1988) and spatially filtered (Gaussian filter: 4 mm FWHM). After normalization, the 3D anatomical data were averaged across subjects. From this average brain ( $n = 15$ ), the cortical surface was segmented, smoothed, inflated and flattened.

For the group analysis, the experimental effects in the different conditions were compared by employing a random-effects general linear model.  $p$ -Values were corrected for multiple comparisons using the false discovery rate as determined by the Benjamini & Hochberg rule (Benjamini & Hochberg, 1995). For each individual subject, four bilateral cortical areas were defined following functional and anatomical criteria. The ROIs were selected on the basis of one experimental scan as a contiguous set of voxels that were significantly ( $p < 0.001$ ) stronger activated in the experimental conditions (Object Identification and Orientation Judgment) compared to fixation. fMRI responses in the other three experimental scans were extracted by averaging the data from all the voxels within the independently defined ROIs. The signal time-course was averaged across scans for each subject and across subjects. Timepoints 3–21 s after the start of a block were selected to characterize the magnitude of the fMRI response within a block. The lag of 3 s is to account for the well-described hemodynamic lag in the fMRI response (Boynton, Engel, Glover, & Heeger, 1996). The magnitude of the fMRI responses were compared across conditions by employing repeated measurements ANOVAs with factor task as within-subject factor. Post-hoc comparisons were conducted using paired  $t$ -tests (two-tailed).

### 3. Results

#### 3.1. Behavioral data

Behavioral data were acquired during the experiments in the scanner. A repeated measurements ANOVA in Experiment 1 with factor task as within-subject factor (Object Identification, Orientation Judgment, Object Identification – Color Control, Orientation Judgment – Color Control) did not reveal significantly different percent correct rates between tasks (Object Identification: 97.0%; Orientation Judgment: 96.6%;  $F[3,42] < 1$ ;  $p = 0.85$ ). However, subjects were significantly slower in judging the orientation in comparison to object identification (Object Identification: 749 ms, S.E.: 71 ms; Orientation Judgment: 840 ms, S.E.: 64 ms;  $F[3,42] = 16.17$ ;  $p < 0.001$ ; Object Identification versus Orientation Judgment:  $t[14] = 4.87$ ,  $p < 0.001$ ).

#### 3.2. fMRI data

##### 3.2.1. Experiment 1

To investigate common and differential spatial distribution of fMRI responses in the Object Identification and Orientation Judgment tasks, we conducted a random-effects GLM analysis, depicted in Fig. 2a. The data showed significant ( $p_{\text{cor}} < 0.05$ ) bilateral activation for the Object Identification versus the fixation period in the early visual areas, higher ventro-temporal visual areas (lateral occipital and within the fusiform gyrus), in parietal regions (within the intraparietal and post-central sulcus) and frontal areas. Significant fMRI responses ( $p_{\text{cor}} < 0.05$ ) for the Orientation Judgment task versus the fixation epochs were found in similar brain regions (Fig. 2a).

To investigate differences between the fMRI responses for Object Identification and Orientation Judgment across the whole cortex, we conducted a random-effects GLM. We observed significantly stronger responses for the Orientation Judgment versus Object Identification ( $p_{\text{cor}} < 0.05$ ) in both hemispheres in lateral occipital regions, along the intraparietal sulcus and frontal areas (Fig. 2b). Importantly, we did not observe significantly stronger fMRI responses for the Object Identification versus Orientation Judgment.

To compare within-subject differences between Object Identification and Orientation Judgment and to assess their robustness, we selected for each subject four, in most subjects bilaterally organized regions of interest (ROIs). Specifically, we selected a ventral temporal–occipital region (vTO, bilateral in 15/15 subjects), a lateral occipital region (LO, bilateral in 14/15 subjects, left lateralized in 1 subject), a region within the intra-parietal sulcus (IPS, bilateral in 13/15 subjects, left lateralized in 1 subject and right lateralized in 1 subject) and in the post-central sulcus (pCS, bilateral in 11/15 subjects, left lateralized in 4 subjects) found to present significantly stronger ( $p < 0.001$ ) activation in the experimental conditions (Object Identification and Orientation Judgment) versus fixation. Table 1 lists the coordinates of the ROIs in the standard system of Talairach and Tournoux (1988).

As shown in Fig. 3, the fMRI responses were significantly stronger in the Orientation Judgment than in Object Identification blocks in vTO ( $F[3,42] = 7.25$ ;  $p < 0.001$ ;  $t[14] = 4.52$ ,  $p < 0.001$ ), LO ( $F[3,42] = 6.53$ ;  $p < 0.01$ ;  $t[14] = 6.44$ ,  $p < 0.001$ ), and in the parietal regions of interest (IPS:  $F[3,42] = 5.44$ ;  $p < 0.01$ ;  $t[14] = 7.05$ ,  $p < 0.001$ ; pCS:  $F[3,42] = 9.21$ ;  $p < 0.001$ ;  $t[14] = 4.58$ ,  $p < 0.001$ ). To investigate differences across hemispheres, we conducted repeated measurement ANOVAs with within-subject factors Task (Orientation Judgment or Object Identification) and Hemisphere (left or right). We did not observe interactions between the two factors in any of the ROIs (vTO:  $F[1,14] < 1$ ,  $p = 0.45$ ; LO:  $F[1,13] < 1$ ,  $p = 0.94$ ; IPS:  $F[1,12] < 1$ ,  $p = 0.70$ ; pCS:  $F[1,10] < 1$ ,  $p = 0.71$ ) which suggests a homogenous distribution of processing between the two hemispheres during Orientation Judgment and Object Identification.

3.2.2. Color control task

To ensure that the observed differences between the Object Identification and Orientation Judgment block cannot be accounted for by differences in stimulation, subjects performed an additional color matching task on the same stim-

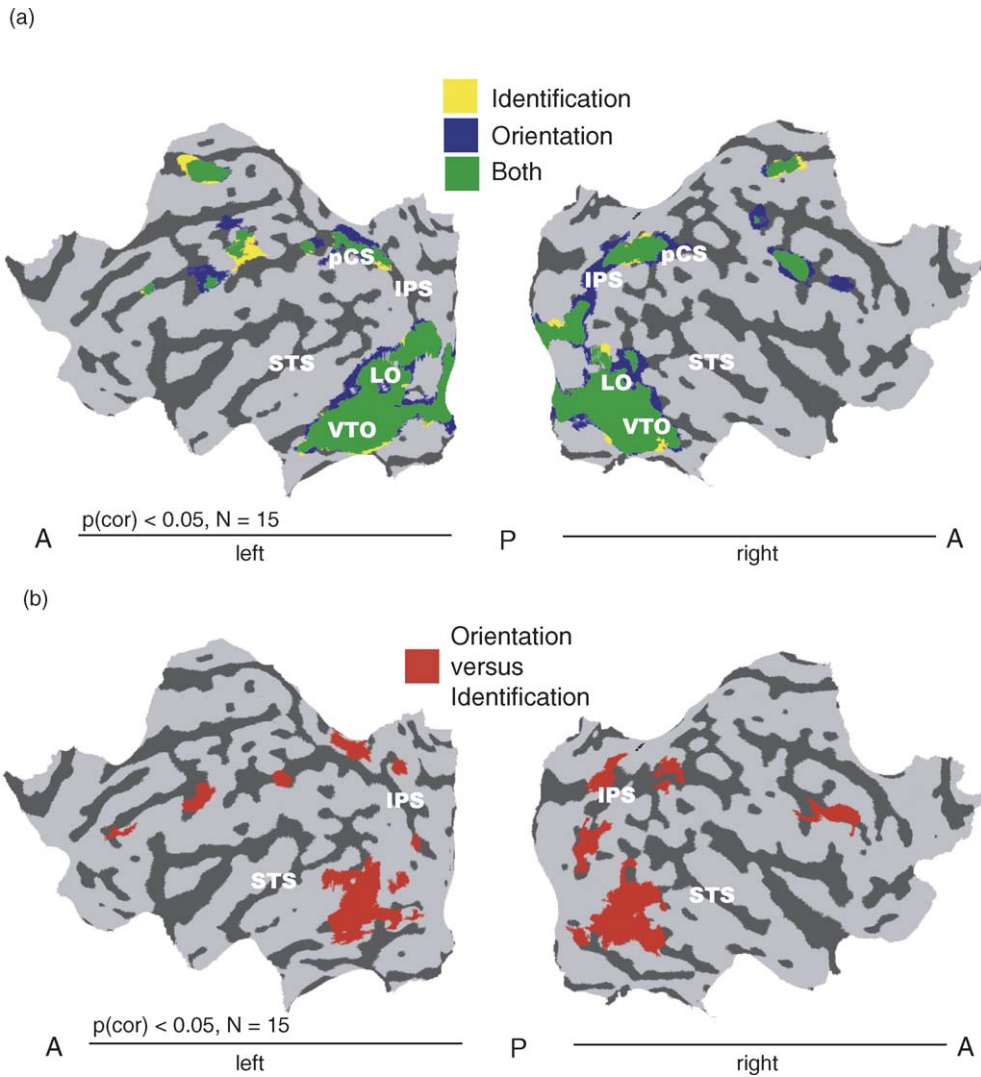


Fig. 2. (a) fMRI responses for Object Identification vs. fixation and Orientation Judgment vs. fixation. Group data ( $n = 15$ ) projected onto a flattened map of the group average cortical surface ( $n = 15$ ). Gyri are shown in light gray, sulci in dark gray. The activation map shows voxels that are significantly stronger ( $p < 0.05$ , FDR-corrected for multiple comparisons) responding in the Object Identification blocks vs. fixation colored in yellow, and voxels that are significantly stronger responding in the Orientation Judgment blocks vs. fixation in blue. Overlap is marked with green color. (b) fMRI responses for Orientation Judgment vs. Object Identification. Group data ( $n = 15$ ) projected onto a flattened map of the group average cortical surface ( $n = 15$ ). The activation map shows voxels that are responding significantly stronger ( $p < 0.05$ , FDR-corrected for multiple comparisons) in the Orientation Judgment vs. the Object Identification blocks colored in red. We did not observe voxels that responded significantly stronger in the opposite contrast, i.e. Object Identification vs. the Orientation Judgment blocks. A: anterior; P: posterior; STS: superior temporal sulcus; vTO: ventral temporal occipital; LO: lateral occipital; IPS: intraparietal sulcus; pCS: post-central sulcus.

Table 1

Talairach coordinates for the selected regions of interest (ROIs) that had significantly stronger fMRI responses in the Object Identification and Orientation Judgment blocks vs. fixation

	Right hemisphere			Left hemisphere		
	x	y	z	x	y	z
vTO	32.9 ± 4.2	-47.6 ± 4.7	-18.4 ± 4.1	-33.3 ± 2.7	-50.6 ± 5.4	-19.0 ± 3.7
LO	39.6 ± 5.4	-66.9 ± 6.3	-10.4 ± 4.7	-41.8 ± 4.2	-67.5 ± 6.5	-8.7 ± 8.3
IPS	28.3 ± 3.4	-70.7 ± 6.4	23.7 ± 8.3	-26.8 ± 4.4	-69.1 ± 7.8	22.8 ± 7.5
pCS	34.3 ± 7.3	-47.7 ± 7.4	44.2 ± 7.7	-36.1 ± 5.3	-45.3 ± 7.1	43.9 ± 8.4

vTO: ventral temporal–occipital cortex; LO: lateral occipital area; IPS: intraparietal sulcus; pCS: post-central sulcus. Talairach coordinates are given in mm, plus and minus standard deviation.

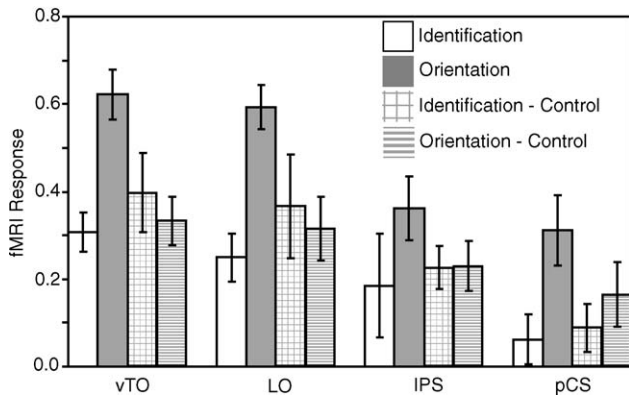


Fig. 3. fMRI responses in vTO, LO, IPS, pCS from Experiment 1 averaged across 15 subjects, taken from 3 to 21 s after the onset of a block. The regions of interest were selected as contiguous areas that had significantly ( $p < 0.001$ ) stronger fMRI responses in the Object Identification and Orientation Judgment blocks versus fixation. The error bars represent mean standard errors of the fMRI responses.

ulus set used in both the Object Identification and Orientation Judgment task. A random-effects GLM did not reveal voxels that showed significantly different responses ( $p_{\text{cor}} < 0.05$ ) for the Orientation Judgment and Object Identification Color Control blocks. Particularly, no significant differences of fMRI responses have been observed in the ventral temporal–occipital (vTO:  $t[14] < 1$ ,  $p = 0.53$ ), lateral occipital regions (LO:  $t[14] < 1$ ,  $p = 0.67$ ), IPS (IPS:  $t[14] < 1$ ,  $p = 0.95$ ) and pCS (pCS:  $t[14] = 1.37$ ,  $p = 0.19$ ). This indicates that the significant differences in fMRI responses observed between the Object Identification and to the Orientation Judgment condition were not caused by differences in visual stimulation between the two tasks.

Interestingly, fMRI responses during Orientation Judgment were significantly stronger compared to the Color Control task in ventral stream areas (vTO:  $t[14] = 4.23$ ,  $p < 0.001$ ; LO:  $t[14] = 4.49$ ,  $p < 0.001$ ) and pCS (pCS:  $t[14] = 2.81$ ,  $p < 0.05$ ), but not in IPS (IPS:  $t[14] < 1$ ,  $p = 0.39$ ). This observation is in agreement with recent fMRI studies (Pins, Meyer, Foucher, Humphreys, & Boucart, 2004) that found more pronounced fMRI activity in the posterior and medial parts of the fusiform gyrus during an orientation-matching task compared to a color matching task. However, our results do not show significantly stronger fMRI responses during the Object Identification task compared to its Color Control task (vTO:  $t[14] = 1.06$ ,  $p = 0.30$ ; LO:  $t[14] = 1.26$ ,  $p = 0.23$ ; IPS:  $t[14] < 1$ ,  $p = 0.37$ ; pCS:  $t[14] = 1.37$ ,  $p = 0.67$ ).

### 3.2.3. Experiment 2

To further attain that differences between the Object Identification and Orientation Judgment obtained in Experiment 1 cannot be accounted for by differences in visual stimulation or task difficulty, we conducted a control experiment in 10 of the 15 subjects that participated in Experiment 1. Subjects were required to match object identity across different orientations and to match orientation across different objects.

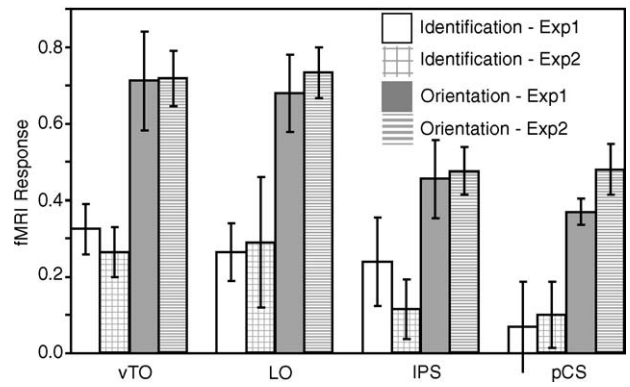


Fig. 4. fMRI responses in vTO, LO, IPS, pCS from Experiments 1 and 2 averaged across 10 subjects, taken from 3 to 21 s after the onset of a block. The error bars represent mean standard errors of the fMRI responses.

As a consequence, performance was at a lower level compared to the first experiment. When we compared the Orientation Judgment task with the Object Identification task, subjects performed less accurately (Object Identification: 94.5%; Orientation Judgment: 81.9%;  $F[2,18] = 13.8$ ;  $p < 0.001$ ; Orientation Judgment versus Object Identification:  $t[9] = 2.97$ ;  $p < 0.05$ ) and at a slower reaction rate (Object Identification: 778 ms, S.E.: 60 ms; Orientation Judgment: 887 ms, S.E.: 71 ms;  $F[2,18] = 40.5$ ;  $p < 0.001$ ; Orientation Judgment versus Object Identification:  $t[9] = 5.64$ ;  $p < 0.001$ ). Thus, the Object Identification and Orientation Judgment tasks in Experiment 2 were matched in terms of visual stimulation but were confounded with task difficulty. However, comparison between the two experiments showed that reaction times were significantly slower in the Object Identification task in Experiment 2 compared to Experiment 1 ( $t[9] = 2.49$ ;  $p < 0.05$ ), but were not significantly different between the Object Identification task in Experiment 2 and the Orientation Judgment in Experiment 1 ( $t[9] < 1$ ;  $p = 0.46$ ). If the observed differences of fMRI responses in Experiment 1 were based on task difficulty, fMRI responses to the Object Identification in Experiment 2 should be similar to those during the Orientation Judgment in Experiment 1, because the two conditions were matched in terms of performance. However, as illustrated in Fig. 4, the fMRI responses during the Orientation Judgment task in Experiment 1 were significantly stronger compared to the Object Identification task in Experiment 2 in both ventral (vTO:  $t[9] = 3.47$ ,  $p < 0.01$ ; LO:  $t[9] = 4.08$ ,  $p < 0.01$ ) and dorsal stream areas (IPS:  $t[9] = 4.25$ ,  $p < 0.01$ ; pCS:  $t[9] = 4.50$ ,  $p < 0.01$ ). This indicates that the pronounced fMRI activity during Orientation Judgment compared to Object Identification cannot be simply attributed to differences in terms of task difficulty or attentional load.

## 4. Discussion

Our study provides evidence that processing of object identity and object orientation involves similar cortical ar-

eas. During both tasks, ventro-temporal and parietal areas were significantly activated. While we observed significantly stronger responses for the Orientation Judgment versus Object Identification task in ventral temporal–occipital cortex, lateral occipital areas, in the intraparietal and the post-central sulcus, we did not find a cortical site that responded stronger to the Object Identification task.

Our data do not support the idea that two different cortical sites exist, which are exclusively involved in either orientation judgment or object identification (Best, 1917; Turnbull, 1997; Turnbull, Beschin, & Della Sala, 1997). One possible interpretation of our observation with reference to findings in brain-damaged patients may be that in orientation agnosia the lesions affect the most vulnerable parts first, that is the processing of orientation of objects that are seen from non-canonical views (Karnath et al., 2000). In agreement with this hypothesis, recent neurophysiological data (Perrett, Oram, & Ashbridge, 1998) proposed a view-dependent approach to object-recognition, in which objects are represented by neurons tuned to view, orientation and size. Lesion of a cortical network that encodes visual objects in a view-based manner might first disrupt the ability to judge non-canonical orientations, because these views appear less frequently in our natural environment and are thus represented by a smaller number of neurons.

The observation that reaction times were significantly longer during the orientation matching task might lead to the assumption that increased task difficulty resulted in stronger fMRI responses for this condition. However, in a control experiment (Experiment 2), we increased the task difficulty in the Object Identification task, which did not result in a significant increase of fMRI activity in the investigated ROIs. While attentional load might contribute to the stronger fMRI responses for the object orientation matching task in ventro-temporal and parietal areas, the results clearly indicate an involvement of both parietal and ventro-temporal cortex in both tasks.

A further account to explain the differences between the Object Identification and Orientation Judgment tasks in Experiment 1 could be that the two conditions employed different visual stimulation. More specifically, in the Object Identification task, subjects were presented with same or different objects in the upright orientation, while in the Orientation Judgment task subjects were presented with the same objects in same or different orientation. Thus, in the Object Identification task, subjects saw a greater variety than in the Orientation Judgment task, whereas in the Orientation Judgment task the variety of views of an object was greater. In this respect, it is not unlikely that different adaptation effects might have occurred in the two conditions: Cortical sites that represent object identity invariant to their view-point, as has been suggested for ventral–temporal areas (James et al., 2002) should show stronger fMRI activity during the Object Identification task. However, this has not been observed in the present study. Moreover, since no differences were observed between the color control tasks that employed the

same stimulation as the two experimental conditions (Object Identification and Orientation Judgment), it is unlikely that the stronger responses for the Orientation Judgment are a pure effect of different visual stimulation. Nevertheless, in the light of recent studies, which proposed that selectivity and thus fMRI adaptation effects in the human lateral occipital complex can be modulated by attention (Murray & Wojciulik, 2004), it is possible that the lack of adaptation effects in the Color Control task can be explained by diminished attention compared to the Object Identification and the Orientation Judgment task.

Ventro-temporal and lateral occipital regions, in particular a region termed the lateral occipital complex (LOC), have been proposed to be involved in object recognition (Kanwisher, Chun, McDermott, & Ledden, 1996; Malach et al., 1996). These cortical areas have been suggested to encode visual shape information in a global rather than feature based manner (Kourtzi & Kanwisher, 2000), invariant to the cues that define shape (Grill-Spector, Kushnir, Edelman, Itzhak, & Malach, 1998) and invariant to object orientation (James et al., 2002), position and size (Grill-Spector et al., 1999). In contrast, our data suggest that these regions are involved in both Object Identification and Orientation Judgment tasks.

Object recognition not only activated ventral but also dorsal areas in the present study. This is in accordance with the recent proposal that object recognition relies on coordinate transformations and thus involves also the parietal cortex (Graf, submitted for publication; Graf, Kaping, & Bühlhoff, 2005). Previous brain imaging studies likewise reported parietal involvement in object recognition (Faillenot et al., 1997; Kraut, Hart, Soher, & Gordon, 1997; Vanrie et al., 2002). This raises the question whether both intact dorsal and ventral cortical areas are necessary to accomplish Object Identification and Orientation Judgment or whether subjects automatically perform both tasks when encountering the visual image of an object. The latter argument would explain the co-activation of both the ventral and dorsal areas and is in agreement with a recent fMRI study that showed involvement of object-related visual areas during an object orientation and color matching task (Pins et al., 2004). Our own data showed similar fMRI activity during the Object Identification and the Color Control task in object-related areas (vTO, LO), which suggests that subjects processed the object identity even though this was not required during the Color Control task. One way to clarify this question might be to utilize transcranial magnetic stimulation (TMS) to induce virtual lesions. A recent study has shown that TMS in parietal cortex affects spatial processing, in particular mental rotation (Harris & Miniussi, 2003). This indicates that intact parietal areas are a prerequisite for spatial processing of objects. However, it is unclear whether or not parietal areas are necessary for unimpaired object recognition.

In summary, this study provides evidence that dorsal and ventral stream areas are activated with both recognition of objects and spatial judgments. Our findings suggest that object

identification and orientation judgment do not follow strictly separable cortical routes, but rather involve both the dorsal and the ventral stream.

## Acknowledgements

This work was supported by grants from the Deutsche Forschungsgemeinschaft (SFB 550-A4) awarded to H.-O. Karnath and by the Max Planck Society. We would like to thank Hans-Joerg Mast for technical assistance with the data acquisition and Kiley Seymour for fruitful comments on the manuscript.

## References

- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society, Series B*, 57, 289–300.
- Best, F. (1917). Hemianopsie und Seelenblindheit bei Hirnverletzungen. *v. Graefes Archiv für Ophthalmologie*, 93, 49–150.
- Boynton, G. M., Engel, S. A., Glover, G. H., & Heeger, D. J. (1996). Linear systems analysis of functional magnetic resonance imaging in human V1. *Journal of Neuroscience*, 16, 4207–4221.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10, 433–436.
- Bülthoff, H. H., & Edelman, S. (1992). Psychophysical support for a 2D view interpolation theory of object recognition. *Proceedings of the National Academy of Science*, 89, 60–64.
- Corballis, M. C. (1988). Recognition of disoriented shapes. *Psychological Review*, 95, 115–123.
- Faillenot, I., Toni, I., Decety, J., Gregoire, M. C., & Jeannerod, M. (1997). Visual pathways for object-oriented action and object recognition: Functional anatomy with PET. *Cerebral Cortex*, 7, 77–85.
- Ferber, S., Karnath, H.O. (2003). Friedrich Best's case Z with misidentification of object orientation. In C. Code, C.-W. Wallesch, Y. Joannette, & A.R. Lecours (Eds.), *Classic Cases in Neuropsychology*, Vol. II (pp. 191–198). East Sussex: Psychology Press.
- Gauthier, I., Hayward, W. G., Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (2002). Bold activity during mental rotation and viewpoint-dependent object recognition. *Neuron*, 34, 161–171.
- Graf, M., Kaping, D., & Bülthoff, H.H. (2005) Orientation congruency effects for familiar objects: Coordinate transformations in object recognition. *Psychological Science*, 16, 214–221.
- Graf, M. Coordinate transformations in object recognition, submitted for publication.
- Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzhak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron*, 24, 187–203.
- Grill-Spector, K., Kushnir, T., Edelman, S., Itzhak, Y., & Malach, R. (1998). Cue-invariant activation in object-related areas of the human occipital lobe. *Neuron*, 21, 191–202.
- Harris, I. M., Harris, J. A., & Caine, D. (2001). Object orientation agnosia: A failure to find the axis? *Journal of Cognitive Neuroscience*, 13, 800–812.
- Harris, I. M., & Miniussi, C. (2003). Parietal lobe contribution to mental rotation demonstrated with rTMS. *Journal of Cognitive Neuroscience*, 15, 315–323.
- James, T. W., Humphrey, G. K., Gati, J. S., Menon, R., & Goodale, M. A. (2002). Differential effects of viewpoint on object-driven activation in dorsal and ventral streams. *Neuron*, 35, 793–801.
- Kanwisher, N., Chun, M. M., McDermott, J., & Ledden, P. J. (1996). Functional imaging of human visual recognition. *Brain Research Cognitive Brain Research*, 5, 55–67.
- Karnath, H. O., Ferber, S., & Bülthoff, H. H. (2000). Neuronal representation of object orientation. *Neuropsychologia*, 38, 1235–1241.
- Kourtzi, Z., & Kanwisher, N. (2000). Cortical regions involved in perceiving object shape. *Journal of Neuroscience*, 20, 3310–3318.
- Kraut, M. A., Hart, J., Soher, B., & Gordon, B. (1997). Object shape processing in the visual system evaluated using functional fMRI. *Neurology*, 48, 1416–1420.
- Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., et al. (1996). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Science*, 92, 8135–8139.
- Marois, R., Leung, H. C., & Gore, J. C. (2000). A stimulus-driven approach to object identity and location processing in the human brain. *Neuron*, 25, 299–308.
- Marr, D., & Nishihara, H. K. (1978). Representation and recognition of the spatial organization of three-dimensional shapes. *Proceedings of the Royal Society of London*, B200, 269–294.
- Murray, S. O., & Wojciulik, E. (2004). Attention increases neural selectivity in the human lateral occipital complex. *Nature Neuroscience*, 7, 8–10.
- Perrett, D. I., Oram, M. W., & Ashbridge, E. (1998). Evidence accumulation in cell populations responsive to faces: An account of generalisation of recognition without mental transformations. *Cognition*, 67, 111–145.
- Pins, D., Meyer, M. E., Foucher, J., Humphreys, G., & Boucart, M. (2004). Neural correlates of implicit object identification. *Neuropsychologia*, 42, 1247–1259.
- Shepard, R. N., & Cooper, L. A. (1982). *Mental images and their transformations*. Cambridge, MA: MIT Press.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain. 3-dimensional proportional system: An approach to cerebral imaging*. New York: Thieme Medical Publishers.
- Tarr, M. J. (1995). Rotating objects to recognize them: A case study on the role of viewpoint dependency in the recognition of three-dimensional objects. *Psychonomic Bulletin & Review*, 2, 55–82.
- Turnbull, O. H., Beschin, N., & Della Sala, S. (1997). Agnosia for object orientation: Implications for theories of object recognition. *Neuropsychologia*, 35, 153–163.
- Turnbull, O. H. (1997). A double dissociation between knowledge of object identity and object orientation. *Neuropsychologia*, 35, 153–163.
- Ullman, S. (1989). Aligning pictorial descriptions: An approach to object recognition. *Cognition*, 32, 193–254.
- Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, Massachusetts: MIT Press.
- Vanrie, J., Beatse, E., Wagemans, J., Sanaert, S., & Van Hecke, P. (2002). Mental rotation versus invariant features in object perception from different viewpoints: An fMRI study. *Neuropsychologia*, 40, 917–930.
- Vuilleumier, P., Henson, R. N., Driver, J., & Dolan, R. J. (2002). Multiple levels of visual object constancy revealed by event-related fMRI of repetition priming. *Nature Neuroscience*, 5, 491–499.