

Dissociation between Ventral and Dorsal fMRI Activation during Object and Action Recognition

Lior Shmuelof¹ and Ehud Zohary^{1,2,*}

¹Neurobiology Department

Life Science Institute

²Interdisciplinary Center for Neural Computation

Hebrew University

Jerusalem 91904

Israel

Summary

Neuropsychological case studies suggest the existence of two functionally separate visual streams: the ventral pathway, central for object recognition; and the dorsal pathway, engaged in visually guided actions. However, a clear dissociation between the functions of the two streams has not been decisively shown in intact humans. In this study, we demonstrate dissociation between dorsal and ventral fMRI activation patterns during observation of object manipulation video clips. Parietal areas, such as anterior intraparietal sulcus (aIPS) display grasp viewing-dependent adaptation (i.e., fMRI adaptation during repeated viewing of the same object-grasping movement) as well as a contralateral preference for the viewed manipulating hand. Ventral regions, such as the fusiform gyrus, show similar characteristics (i.e., adaptation, contralateral preference), but these depend on object identity. Our results support the hypothesized functional specialization in the visual system and suggest that parietal areas (such as aIPS) are engaged in action recognition, as well as in action planning.

Introduction

One of the most influential concepts in understanding biological vision is the division of labor between the two major visual pathways (Mishkin and Ungerleider, 1982; Livingstone and Hubel, 1988; Goodale and Milner, 1992). It is commonly thought that areas in the ventral pathway, extending from the striate cortex to the inferotemporal cortex, play a major role in object recognition, while the dorsal pathway regions are supposedly engaged in sensorimotor transformation necessary for visually guided actions (Goodale and Milner, 1992). This concept is supported by neuropsychological case studies showing that damage to the ventrolateral part of the occipitotemporal cortex results in agnosia, a severe impairment in the perception of objects, while the ability to accurately grasp the same unidentified objects remains intact (James et al., 2003). Individuals with damage in the superior part of the parietal cortex show the opposite behavior, termed optic ataxia: they are often unable to use visual information to guide their grasping movements. For example, they show poor performance in generating the correct gap between the index finger and thumb before making physical contact

with the target object. However, their ability to visually recognize objects is normal (Goodale et al., 1994). Another source of evidence for the functional separation between perception and action comes from psychophysical studies in healthy human subjects. For example, Aglioti et al. (1995) showed that grasp calibration is insensitive to robust perceptual illusions that result from surround effects (e.g., a target disk surrounded by smaller circles appears larger than the same disk surrounded by circles bigger than itself).

Some indication for the functional separation between the visual pathways in humans can also be seen in recent fMRI studies. James et al. (2002) showed that the ventral object-related regions (ventral occipitotemporal cortex [VOT] and lateral occipital complex [LOC]) exhibit fMRI adaptation when the subject is viewing the same object from different viewpoints, but no such adaptation is found in the dorsal object-related areas (located in the caudal intraparietal sulcus [cIPS]). Culham et al. (2003) showed a complementary effect: visually guided grasping produced higher fMRI activation than reaching movements in the anterior intraparietal sulcus (aIPS), but not in ventral stream brain areas.

To summarize, most of the evidence for the functional division in humans is either based on very few case studies or indirect evidence from psychophysical experiments. Although the fMRI studies mentioned above promote our understanding of the functional dissociation between the two streams, a carefully tailored fMRI study, aimed to provide direct evidence for the functional dissociation between the two visual streams in humans, has not been carried out. We therefore designed an fMRI experiment that could substantiate the claim for the perception/action division, using various analysis methodologies (see below). We took advantage of recent evidence from single unit recordings in monkeys that indicate that some dorsal stream areas (such as the inferior parietal lobule) are active during passive observation of object manipulation by others (Fogassi et al., 2005). Therefore, we studied the patterns of fMRI activation in the human dorsal and ventral pathways during *observation* of video clips showing object manipulation, using three different analysis methods:

1. **Contralateral bias:** The bias toward a contralateral representation of the visual field is a robust characteristic of the visual cortex (Tusa et al., 1979; Mountcastle et al., 1981; Niemeier et al., 2005). We used asymmetric video clips in which a fixation point was located centrally, a hand was seen reaching from the right side, and manipulating objects positioned on the left visual field, or vice versa. We reasoned that areas sensitive to the reaching and grasping aspects should show mainly contralateral activation with respect to the *hand position* (i.e., left hemisphere dominance when the hand is seen approaching from the right side), while areas sensitive to the *object identity* are expected to show the opposite trend (i.e., right hemisphere dominance, since the objects were in the left visual field).

*Correspondence: udiz@lobster.ls.huji.ac.il

2. Task-related activation: Varying the task that the subjects perform while the physical attributes of the visual stimuli remain constant across conditions may result in differences in fMRI activation. The functional separation hypothesis predicts that the dorsal areas will show greater activation during an action-oriented task (in our case, covertly answering how many fingers are involved in the grasping movement) than during an object-oriented task (i.e., covertly naming the object), while the converse is expected in the ventral pathway.
3. fMRI adaptation (Grill-Spector and Malach, 2001): Repetitive presentation of the same visual stimuli results in adaptation of the fMRI signal. We tested whether repeated *observation* of the same grasping *action* (irrespective of the object identity) would lead to adaptation in the dorsal pathway (but not in the ventral areas), while repeated observation of the same *object* (irrespective of the grasping characteristics) would result in adaptation in the ventral stream.

The results from these three methods point toward a dissociation between ventral and dorsal stream fMRI activation during observation of object manipulation. These results support the concept of functional dissociation in the visual system and also suggest that some areas in the parietal cortex (such as the aIPS) may be engaged in action recognition as well as in action planning.

Results

We investigated the patterns of cortical activation using functional magnetic resonance imaging in two block design experiments. Each experiment contained five visual conditions, repeated four times in a counterbalanced manner. The experimental conditions included video clips of ten object manipulations by a single hand. The objects were on one side of the screen, and the grasping hand was mainly seen on the other side of the screen. The objects were stationary in all conditions. A control condition, composed of a spatially scrambled version of one of the object manipulation clips, was used for selection of voxels showing differential activation during the observation of object manipulation clips. The subjects were instructed to maintain fixation on a red point located in the center of the screen throughout the two experiments.

Experiment I

The aim of this experiment was to differentiate between brain areas that are active during *observation of actions* and those involved in *object recognition*. One method we used took advantage of the bias toward a contralateral visual field representation which characterizes the visual system (Tusa et al., 1979; Mountcastle et al., 1981; Niemeier et al., 2005). We generated video clips of object manipulation in which an object is present in the left visual field and the (right) hand, approaching from the right visual field, is seen grasping the object. We term this condition “Right hand/Left object.” In the other condition, the subjects were viewing the mirror

image of those clips (i.e., “Left hand/Right object”). By contrasting the fMRI activation in these two conditions, we reasoned that areas engaged in the processing of objects will show a greater activation in the hemisphere contralateral to the object’s location, whereas areas that are engaged in processing of the hand action (present mainly in the opposite visual field) should display greater activation in the hemisphere contralateral to the hand position.

Another method for dissociating between ventral and dorsal activation was to manipulate the task the subjects performed. The two sets of previously mentioned clips were actually shown twice: once while the subjects performed an object-oriented task, covertly naming the objects (“Name”), and once during performance of an action-oriented task, covertly counting how many fingers interact with the object (“Count”).

The overall experimental design is shown in Figure 1. Eleven subjects were scanned while observing five different conditions: 1, “Left hand/Right object,” performing the task “Count”; 2, “Right hand/Left object,” performing the task “Count”; 3, “Right hand/Left object,” performing the task “Name”; 4, “Left hand/Right object,” performing the task “Name”; 5, spatially scrambled version of the object manipulation clips.

Data were analyzed at two levels: group analysis and ROI analysis. Using group analysis, we show the effects of the asymmetry of the visual display (Figure 2) and task (Figure 4) in whole-brain statistical parameter maps. Subject by subject analysis (ROI analysis) was based on anatomically defined regions of interest (ROIs) within the object manipulation-related areas (showing significantly greater activation during the object manipulation conditions than during the scrambled condition) in each one of the subjects. In each ROI, we compared the fMRI activation during the various conditions, looking for significant differences between them (Figures 3 and 5).

Group Analysis

Figure 2 depicts the effect of the laterality (right hand versus left hand, or equivalently, left object versus right object). Significant preference for the “Right hand/Left object” condition can be seen in *right* ventral occipital areas, such as FuG, and in *left* dorsal occipital areas (cuneus), intraparietal sulcus, and pre-central gyrus. Significant preference for the “Left hand/Right object” clips can be seen in *left* ventral occipital areas, and in *right* dorsal and lateral occipital areas (cuneus, lateral occipital sulcus) and intraparietal sulcus. For details, see Table 1. To summarize, in view of the known contralateral preference in the visual system (Niemeier et al., 2005), we suggest that the activation in the *dorsal* (parietal) areas is determined by the *location of the active hand*, whereas in the *ventral* (occipitotemporal) areas, the activation is dependent on the *location of the viewed objects* (note that both the manipulating hand and the objects are seen in all conditions). The contralateral preference for the active hand in the dorsal areas, as opposed to the object preference in the ventral areas, can also be seen in the majority of the individual subjects (see Figure S2 in the Supplemental Data available online).



Figure 1. Experiment I—Experimental Design

Five conditions were interleaved in a block design experiment. 1. A hand seen approaching from the left side and grasping ten different objects presented on the right side of the screen (termed “Left hand/Right object”). In this condition, the subjects had to count how many fingers interact with the object (“Count”). 2. Mirror image of the “Left hand/Right object” clips (i.e., “Right hand/Left object” clips). The subjects performed the same task (“Count”). 3. “Right hand/left object” video clips, while the subjects had to covertly name the objects (“Name”). 4. “Left hand/right object” clips, the subjects performed the “Name” task. 5. Spatially scrambled version of the object manipulation clips. The subjects were required to maintain fixation on a central dot throughout the experiment.

ROI Analysis

Next, we investigated whether the preference for the objects or the manipulating hand found in the ventral and dorsal areas, respectively, can also be seen in specific regions of interest on a subject by subject basis. A crucial point in such ROI analysis is to assure that the ROI voxels are selected so that no a priori bias is given for one object manipulation condition over the others. We therefore identified object manipulation-related areas in each subject as those showing significantly higher activation in the various object manipulation clips compared to the activation elicited by the

observation of a scrambled version of those clips (all object manipulations > scramble, $p < 0.01$, correction for cluster size). Within those areas we identified in each one of the subjects four regions of interest: two in the vicinity of the intraparietal sulcus (left aIPS [$n = 11$, averaged cluster size = $2184 \pm 286 \text{ mm}^3$] and right aIPS [$n = 11$, averaged cluster size = $1742 \pm 146 \text{ mm}^3$]) and two in the ventral bank of the occipitotemporal cortex (left FuG [$n = 11$, averaged cluster size = $1343 \pm 173 \text{ mm}^3$] and right FuG [$n = 9$, averaged cluster size = $1263 \pm 330 \text{ mm}^3$]; in two subjects, no significant cluster of activation was found in this ROI). Next, we esti-

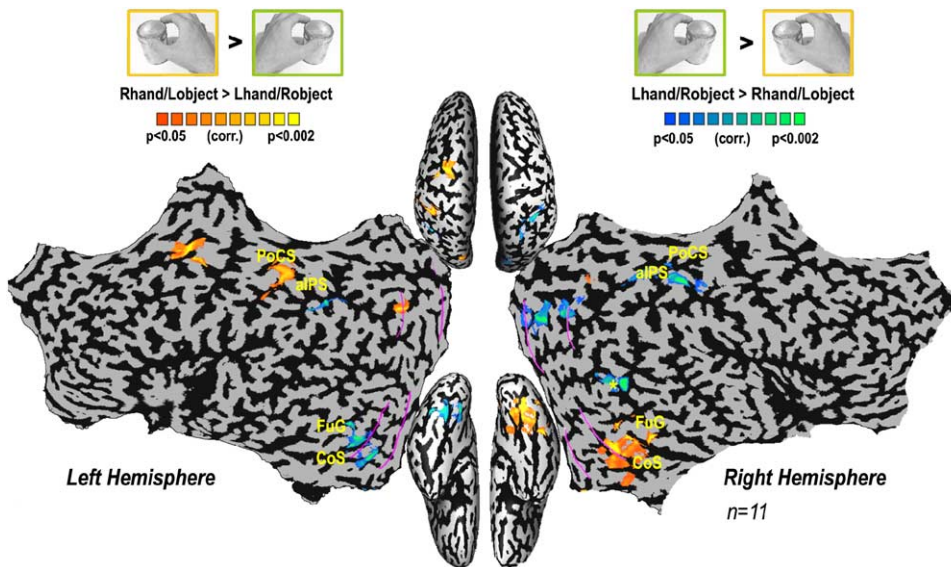


Figure 2. Preference for Hand Action Viewing versus Object Viewing in the Human Cortex

Statistical parametric maps of 11 subjects, using a random effect GLM analysis. Red to yellow colors depict voxels showing increasingly significant preference for the “Right hand/Left object” over the “Left hand/Right object” clips, while voxels in blue to green show the opposite selectivity. Note that the parietal areas such as aIPS and post-central gyrus (PoCG) show preference for the “Right hand/Left object” conditions, in the *left* hemisphere, while in the *right* hemisphere the preference is for the “Left hand/Right object” conditions. Given the contralateral preference in these areas, the activation is determined by the *hand’s position* on the screen. In the ventral areas, such as FuG, an opposite preference can be seen, suggesting that the activation in those areas is determined by the *location of the object*. The posterior purple lines indicate the approximate border between V1 and V2, while the anterior purple lines indicate the estimated anterior border of the retinotopic areas (V3A dorsally, and V4V ventrally). This estimation is based on phase analysis, using the rotating wedge technique in one of the subjects (subject #1). Yellow asterisk denotes the site of the “extrastriate body area,” in the right hemisphere, Talairach coordinates: (50, -70, 4).

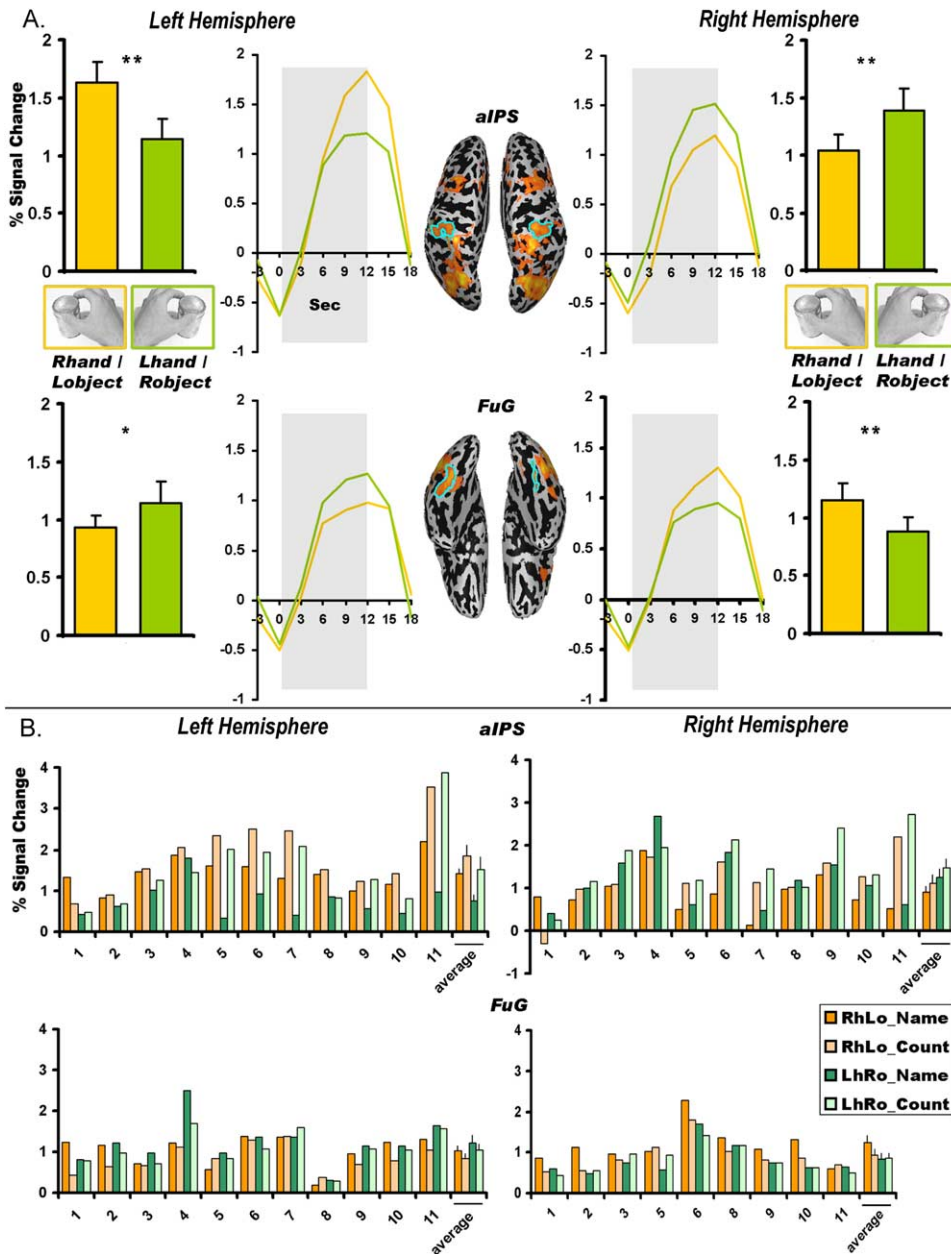


Figure 3. Hand Action Viewing versus Object Viewing—Regions of Interest Analysis

(A) Voxels displaying object manipulation-related activation were selected if anatomically located within two regions of interest (aIPS and FuG, in the two hemispheres) in each of the subjects. Thus, each voxel within these ROIs showed significantly higher activation for the object manipulation clips compared to the scrambled version of the same clips ($p < 0.01$, corrected for cluster size). (Central insets) Ventral and dorsal views of the inflated brain showing the object manipulation-related areas in one of the subjects (subject #2). ROIs are marked in cyan. (Left and right panels) Averaged hemodynamic response curves and bar histograms of the percent signal change for the two object manipulation clips “Left hand/Right object” (green) and “Right hand/Left object” (orange) in the four ROIs: left aIPS ($n = 11$), right aIPS ($n = 11$), left FuG ($n = 11$), and right FuG ($n = 9$). The gray background denotes the time of the condition. Error bars denote SEM. Significant contralateral preference for the location of the hand can be seen in the aIPS, bilaterally. Significant contralateral preference for the object’s position on the screen can be seen in the FuG, bilaterally. Asterisks denote significance ($*p < 0.05$; $**p < 0.01$).

(B) Single-subject fMRI activation in the object manipulation-related areas in aIPS and FuG. The bars depict the activation in each one of the subjects for the four object manipulation conditions: Right hand/Left object under the task Name (“RhLo_Name”), Left hand/Right object under the task Name (“LhRo_Name”), Right hand/Left object under the task Count (“RhLo_Count”), Left hand/Right object under the task Count (“LhRo_Count”). The rightmost columns in each ROI depict the group average activation in the ROI. Error bars denote SEM.

ated the average percent signal change for each condition in the different ROIs. Figure 3A depicts the average percent signal change of the two “Right hand/Left ob-

ject” conditions (averaged across the two tasks) and the two “Left hand/Right object” conditions.

The results are consistent with the results of the

Table 1. Brain Regions Showing Significantly Greater Activation during “Right Hand/Left Object” Clips than during “Left Hand/Right Object” Clips or Vice Versa

Area Name	Talairach Coordinates			Cluster Size (mm ³)	Cluster Analysis		BA
	X	Y	Z		Averaged T Value	p Value	
RH, fusiform gyrus	26	-56	-10	5447	3.009 (Rh/Lo)	0.02	19
RH, dorsal occipital	14	-79	34	852	2.88 (Rh/Lo)	0.022	19
LH, fusiform gyrus	-22	-58	-7	3655	2.81 (Lh/Ro)	0.024	19
LH, dorsal occipital	-11	-79	38	790	2.74 (Rh/Lo)	0.026	19
RH, cuneus	3	-75	24	646	3.02 (Lh/Ro)	0.018	18
RH, cuneus	5	-75	8	811	2.656 (Lh/Ro)	0.029	18
LH, superior temporal gyrus	-38	-52	31	381	2.94 (Lh/Ro)	0.021	39
RH, lateral occipital sulcus	43	-64	6	698	3 (Lh/Ro)	0.02	37
RH, superior parietal lobule	24	-50	63	705	2.97 (Lh/Ro)	0.022	7
RH, IPS	20	-69	53	976	2.81 (Rh/Lo)	0.023	7
RH, anterior IPS	32	-37	55	1849	2.8 (Lh/Ro)	0.025	40
LH, anterior IPS	-36	-42	54	2459	2.86 (Rh/Lo)	0.023	40
LH, middle frontal gyrus	-27	-10	58	2075	3.12 (Lh/Ro)	0.019	6

p < 0.05 (corrected). “Rh/Lo”: preference for the “Right hand/Left object” clips. “Lh/Ro”: preference for the “Left hand/Right object” clips. Talairach coordinates denote the cluster’s center of mass. T values and p values denote averages across the cluster’s voxels.

group analysis. In the left aIPS, the activation is significantly higher for the condition “Right hand/Left object” than its mirror image (left aIPS, $t = 8.2$, $p < 0.001$), while in the right aIPS, the activation is significantly greater for the condition “Left hand/Right object” (right aIPS, $t = 4.82$, $p < 0.001$). The complementary picture was found in the FuG: significant preference for the “Left hand/Right object” condition can be seen in the left hemisphere ($t = 2.36$, $p < 0.04$), while in the right FuG, the preference is for the “Right hand/Left object” condition ($t = 3.95$, $p < 0.003$). These results show that, while both ventral and dorsal regions are activated during observation of object manipulation clips, the dorsal region of choice (aIPS) shows a contralateral preference for the hand action, whereas in the ventral ROI (FuG), the contralateral activation is determined by the object’s location. To illustrate the degree of consistency of this result between subjects, we also show the level of activation in each of the subjects during the four conditions. The contralateral preference shown in the averages across the two tasks (Figure 3A) is also evident in the single subjects’ activation profile, irrespective of the task performed (Figure 3B).

Another technique that we used to show dissociation between ventral and dorsal activations was through manipulation of the task. Our prediction was that, in the dorsal areas, an action-oriented task will induce higher activation than the object-oriented task, while an object-oriented task will induce higher activation in the ventral areas.

Figure 4 shows the results of group analysis. Significant preference for the action-oriented task (“Right hand/Left object” under the task “Count” + “Left hand/Right object” under the task “Count” > “Right hand/Left object” under the task “Name” + “Left hand/Right object” under the task “Name”) can be seen in the vicinity of the intraparietal sulcus, such as aIPS and post-central gyrus, bilaterally. Significant preference for the object-oriented task (the reverse contrast) can be seen in ventral occipital areas, such as FuG. For details, see Table 2.

We also measured the task-related changes in the

fMRI signal in the ventral and dorsal ROIs (aIPS and FuG). The graphs in Figure 5 depict the average percent signal change (averaged across the two mirror conditions) during performance of each task. Consistent with the group analysis, preference for an object-oriented task (over the action-oriented one) can be seen in the ventral ROIs (right FuG, $t = 2.45$, $p < 0.02$; left FuG, $t = 2.83$, $p < 0.02$), while the reverse picture (preference for the action-oriented task) can be seen in the dorsal ROIs (right aIPS, $t = 1.84$, $p < 0.1$; left aIPS, $t = 2.57$, $p < 0.03$). Thus, in spite of the fact that the video clips were exactly the same, we found dissociation between the dorsal and ventral activations, which were solely governed by the attentional requirements.

Experiment II

After showing dissociation between the dorsal and ventral activation during action observation, using the contralateral bias and task-related activation, we wanted to validate and further explore the separation between the representation of hand action and objects using the fMRI adaptation paradigm. In experiment I, we found evidence that the dorsal areas may be involved in the representation of the hand action. However, we cannot say which element of the hand action is represented in those areas—is it the hand, the interaction between the hand and the object, or motion per se? In the current experiment we investigated whether the representation in these areas is sensitive to properties of the grasping movements made upon the objects. If this is the case, repeated observation of the same grasping action (irrespective of the object identity) would lead to adaptation in the dorsal pathway (but not in the ventral areas), while repetition of the same object (irrespective of the grasping characteristics) would result in adaptation in the ventral stream. To investigate the importance of the observed interaction between the hand and the object, we added another condition, showing clips of pointing movement, in which similar hand motion was seen but there was no physical contact between the hand and the object.

The overall experimental design is shown in Figure 6.

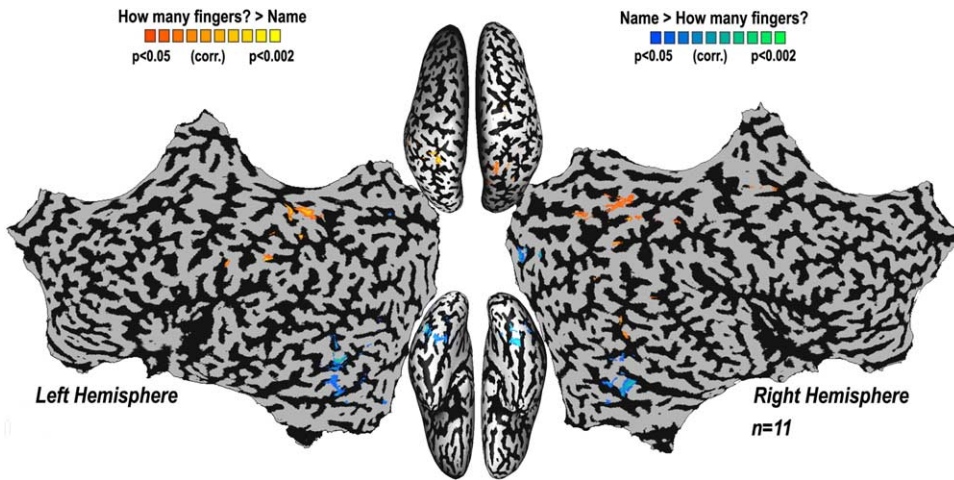


Figure 4. Task-Dependent Modulation: Object-Oriented Task versus Action-Oriented Task

Statistical parametric maps of 11 subjects, using random effect GLM analysis, contrasting the fMRI activation elicited by the two different tasks (while viewing identical visual stimuli). Voxels showing significant preference for the action-oriented conditions (“Right hand/Left object” and “Left hand/Right object”, under the task “How many fingers?”) compared to the object-oriented conditions (“Right hand/Left object” and “Left hand/Right object”, under the task “Name”) are shown in red to yellow. Voxels showing the opposite preference are shown in blue to green. There is a marked preference for the action-oriented task in the vicinity of the intraparietal sulcus, bilaterally, and for the object-oriented task in ventral occipital areas, bilaterally.

The same eleven subjects were scanned while observing five conditions. In all conditions, the object was located on the left side of the screen, and the hand was mainly on the right side of the screen. The conditions were as follows: 1, ten similar grasping movements of the same object (termed “Same object/Same grasp”; SoSg); 2, ten different grasping movements of the same object (“Same object/Different grasp”; SoDg); 3, same grasping movement of ten different objects (“Different object/Same grasp”; DoSg); 4, ten different grasping movements of ten different objects (“Different object/Different grasp”; DoDg); 5, ten identical pointing movements toward the same object (“Point”). Analysis of the first four conditions allowed us to measure the effect of two adaptation factors: object-based adaptation and grasp viewing-based adaptation.

Figure 7 depicts the results of a group analysis using

GLM analysis for two separate contrasts: same objects versus different objects (irrespective of grasping similarity; DoDg + DoSg > SoSg + SoDg), indicating object-based adaptation; and same grasp versus different grasp (irrespective of object similarity; DoDg + SoDg > SoSg + DoSg), indicating grasp viewing-based adaptation. Voxels depicted in blue are ones showing significant object-based adaptation, whereas pink voxels are ones showing grasp-based adaptation. Voxels showing both effects are displayed in cyan. Robust object-based adaptation can be seen in the occipital lobe, both in dorsal and ventral areas, and in the vicinity of the intraparietal sulcus of the left hemisphere. Grasp (viewing)-based adaptation can be seen in the vicinity of the intraparietal sulcus, bilaterally, in the left post-central gyrus, and in the pre-central gyrus.

The asymmetry in the adaptation found in the two

Table 2. Brain Regions Showing Significantly Greater Activation during “Count” Task than during the “Name” Task or Vice Versa

Area Name	Talairach Coordinates			Cluster Size (mm ³)	Cluster Analysis		BA
	X	Y	Z		Averaged T Value	p Value	
RH, fusiform gyrus	32	-64	-9	492	2.69 (Name)	0.028	19
RH, lingual gyrus	3	-79	3	847	2.69 (Name)	0.026	1
RH, fusiform gyrus	28	-50	-10	774	2.75 (Name)	0.025	37
LH, lingual gyrus	-29	-75	-5	523	2.73 (Name)	0.026	1
LH, fusiform gyrus	-33	-55	-9	1263	2.62 (Name)	0.029	37
RH, middle temporal gyrus	45	-58	10	453	2.74 (Count)	0.027	39
RH, superior parietal lobule	13	-67	55	946	2.66 (Count)	0.03	7
LH, superior parietal lobule	-33	-56	56	595	2.82 (Count)	0.024	7
RH, anterior IPS	35	-48	56	871	2.84 (Count)	0.023	40
LH, anterior IPS	-37	-44	50	605	2.62 (Count)	0.09	40
LH, post-central gyrus	-56	-24	34	501	3.11 (Count)	0.02	2

p < 0.05 (corrected). “Name”: preference for the object-oriented task (name the object). “Count”: preference for the action-oriented task (how many fingers interact with the object?). Talairach coordinates denote the cluster’s center of mass. T values and p values denote averages across the cluster’s voxels.

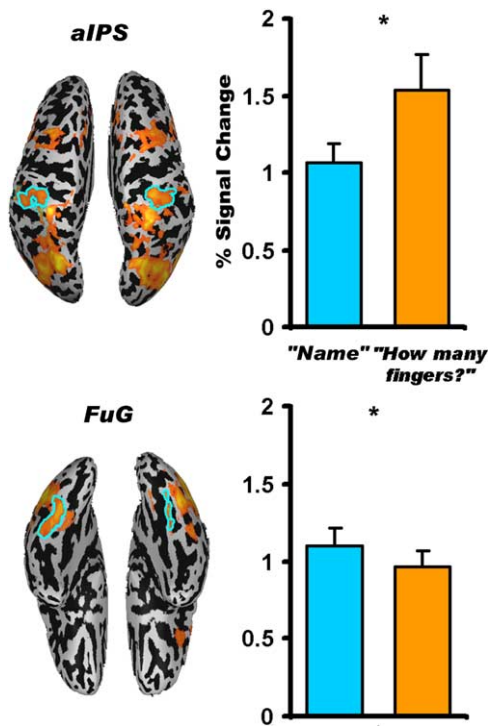


Figure 5. Object-Oriented Task versus Action-Oriented Task—Regions of Interest Analysis

ROI analysis of the fMRI activation elicited by the two different tasks (in aPS and FuG, combined across the two hemispheres). (Left panel) Ventral and dorsal views of inflated cortical maps showing the object manipulation-related areas in one of the subjects (subject #2). ROIs are marked in cyan. (Right panel) fMRI activation change in the two tasks ($n = 11$): action-oriented task (“How many fingers?”, shown in orange) and object-oriented task (“Name,” shown in cyan). Error bars denote SEM. Significant preference for action-oriented task can be seen in the aPS, and for the object-oriented task in the FuG. Asterisks denote significance ($*p < 0.05$).

hemispheres, manifest in a much broader object-based adaptation in the occipital lobe of the right hemisphere, is probably due to the asymmetric nature of the video

clips, which always showed the right hand reaching and grasping objects placed on the left side of the fixation point. Thus, due to the typical contralateral nature of activation in the occipital cortex, object-based adaptation was broader in the right hemisphere.

ROI Analysis

In the group analysis, we found evidence for object-based adaptation in the occipital and temporal lobes and for grasp-based adaptation in the parietal lobe. To further explore this distinction, we assessed, on a subject by subject basis, the magnitude of two factors (i.e., object identity and grasp characteristics) in selected object- and grasp-related areas. Object-related areas were identified as those showing significantly greater activation during viewing of *different* objects (that were similarly grasped; i.e., DoSg) than during viewing of the *same* objects (grasped in the same way; i.e., SoSg), thus exhibiting object-based adaptation ($p < 0.05$, corrected). Analogously, grasp-related areas were identified as those showing significant adaptation ($p < 0.05$, corrected) governed by the grasp identity (i.e., significantly greater activation during *different grasping* of the same object [SoDg] than during the *same grasping* of the same object [SoSg]).

Selection of the ROI voxels was based on both anatomical and functional criteria: object-related voxels were chosen individually in each subject if they were within the FuG and showed object-based adaptation. Analogously, grasp-related voxels were chosen if they were within the aPS and showed grasp-based adaptation. Figure 8 shows the average activation pattern of the object- and grasp-related voxels within the FuG and aPS, respectively. If the two factors—object and grasp identity—are analyzed separately in the two visual pathways, we would expect to find minimal or no grasp-based adaptation in the object-related areas, and analogously, limited object-based adaptation in the grasp-related areas. Since the ROIs were selected according to their adaptation properties in one domain (object adaptation in the ventral regions and grasp-

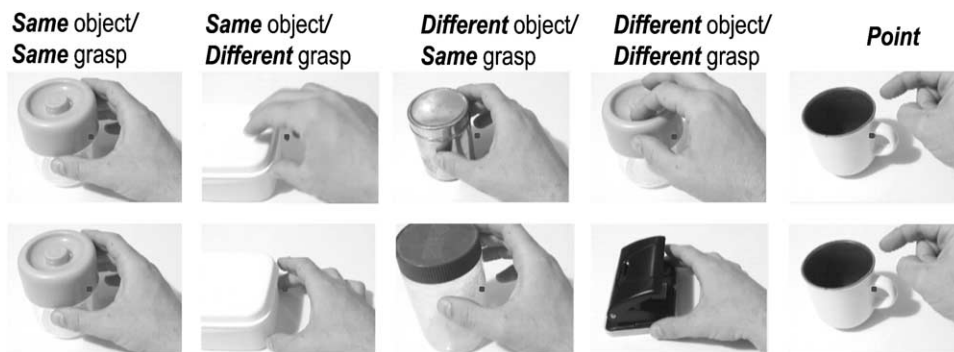


Figure 6. Experiment II—Experimental Design

Five conditions were interleaved in a block design experiment: 1. A hand seen approaching from the right, repeating the same grasping movement on the same object ten times (termed Same object/Same grasp; SoSg). 2. The hand is seen making ten different grasping movements on the same object (Same object/Different grasp; SoDg). 3. The hand is seen making the same grasping movement on ten different objects (Different object/Same grasp; DoSg). 4. The hand is seen making ten different grasping movements on ten different objects (Different object/Different grasp; DoDg). 5. The hand is seen making ten repetitive pointing movements toward the same object. The subjects were required to maintain fixation throughout the experiment.

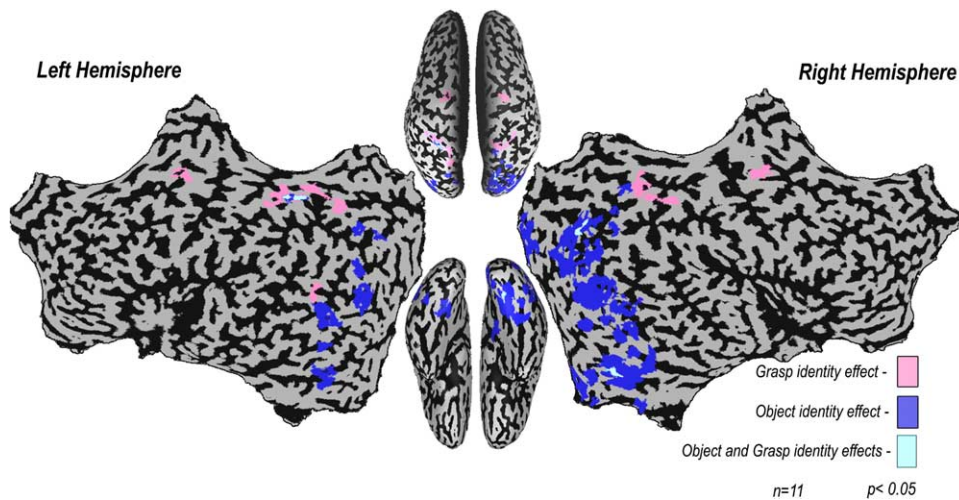


Figure 7. Object- and Grasp-Based Adaptation Effects

Statistical parametric maps of 11 subjects, using random effect GLM analysis. The maps depict two separate effects: object-based adaptation (blue voxels), indicating the voxels that were significantly more active during observation of different objects (i.e., conditions DoDg, DoSg) than during observation of the same object (SoSg, SoDg). Grasp-based adaptation (pink voxels), indicating the voxels that showed significantly higher activation during observation of different grasp movements (DoDg, SoDg) than during observation of the same grasp movement (SoSg, DoSg). Cyan signifies the voxels that show the two effects. Object-based adaptation can be seen in the occipital lobe, both in dorsal and ventral areas, and in the intraparietal sulcus of the left hemisphere. Grasp-based adaptation can be seen in parietal areas, especially in the left intraparietal sulcus, and post-central gyrus, bilaterally, and in the frontal lobe, in the pre-central gyrus.

viewing adaptation in the dorsal ones), the focus of this analysis is naturally on the magnitude of the adaptation due to the *other* factor in each ROI (i.e., object-based adaptation in the aIPS and grasp-based adaptation in the FuG). In the ventral ROIs, we did not find significant grasp-based adaptation in the left FuG ($t = 0.35$, $p < 0.8$), while marginally significant grasp-based adaptation was found in the right FuG ($t = 2.183$, $p < 0.06$). In the dorsal ROIs, no significant adaptation was found in the right aIPS ($t = 1.4$, $p < 0.21$), but some object-based adaptation was found in the left aIPS ($t = 2.27$, $p < 0.05$).

To summarize, both group and the single-subject analyses indicate that the patterns of adaptation in FuG are foremost according to the object identity, while in aIPS, the adaptation is primarily governed by the grasping similarity. In left aIPS, however, the adaptation due to both grasping similarity and object identity reached significant levels, but the former was more prominent.

Finally, we wished to verify that this pattern of adaptation characterizes the *specific* object manipulation-related areas (aIPS and FuG) as defined in experiment 1. These ROIs were defined as having greater activation during object manipulation viewing compared to visual control. This allows examining the degree of congruence of the results *across experiments*, as these ROIs showed a contralateral preference for the representation of hand actions in the aIPS and objects in FuG, as well as modulation of the activation according to the nature of the preferred task in the two areas. The significance of the two adaptation factors (grasp based, object based) was assessed in these ROIs using a repeated-measures analysis of variance (see also the fMRI activation results of each individual in Figure S1). In congruence with the previous analyses, we found

that the grasping factor proved to be significant in *right aIPS* ($F_{1,10} = 18.865$, $p < 0.001$, partial eta squared, $\eta_p^2 = 0.654$) and *left aIPS* ($F_{1,10} = 25.496$, $p < 0.001$, $\eta_p^2 = 0.718$), while the *object* factor was significant in *left FuG* ($F_{1,10} = 33.343$, $p < 0.001$, $\eta_p^2 = 0.769$), *right FuG* ($F_{1,8} = 30.123$, $p < 0.001$, $\eta_p^2 = 0.790$). As in the previous ROI analysis, however, object identity was also a significant factor affecting the magnitude of the response in the *left aIPS*, but to a lesser extent than the grasping type ($F_{1,10} = 7.457$, $p < 0.03$, $\eta_p^2 = 0.427$).

These converging results indicate that the areas that demonstrate a clear contralateral preference for representation of objects and hand actions also manifest congruent patterns of adaptation. Specifically, in the aIPS, where there is clear preference for the representation of the contralateral hand, there is also significant adaptation, governed by the degree of grasping similarity. Similarly, the ventral visual areas, which showed clear preference for representation of objects in the contralateral visual field, showed significant object-based adaptation.

Is the hand-object interaction the critical factor, driving the activation in the dorsal areas? To test this issue, we compared the activation during the “Point” condition and the “Same object/Same grasp” (SoSg) condition in the anatomically defined object- and grasp-related areas (see Figure 8). In both conditions, the subject watched the same footage repeatedly, the only difference was that in the SoSg condition the hand grasped the object, whereas in the “Point” condition the hand was seen approaching the object while making a pointing movement, but did not touch it. We reasoned that if the dorsal areas are engaged in the representation of the grasping movements, i.e., in hand-object interaction, we would expect to find differences

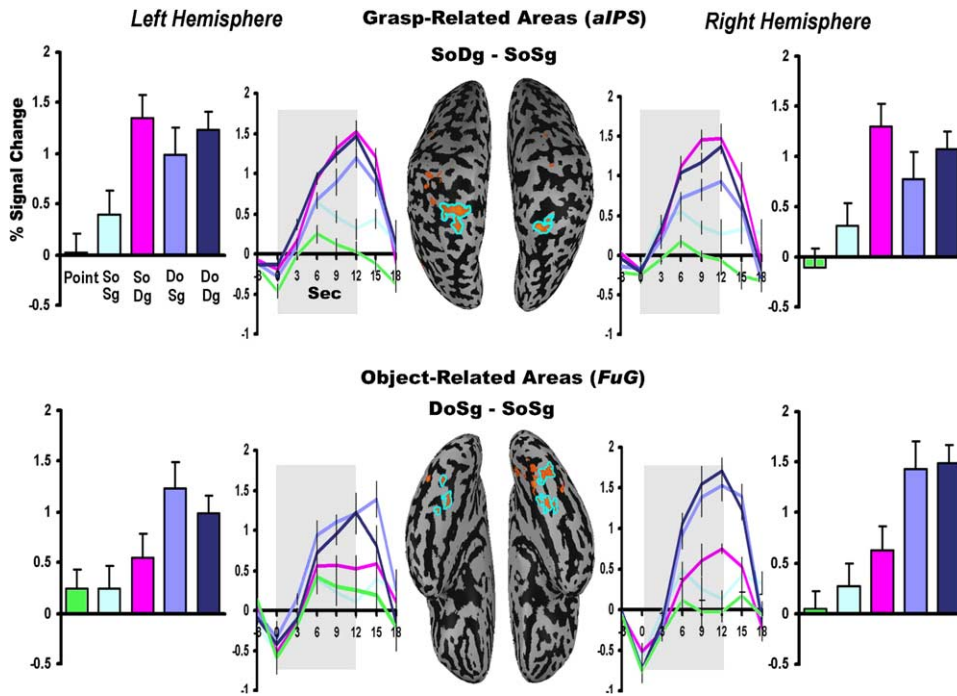


Figure 8. Object and Grasp Identity Adaptation Effects—Regions of Interest Analysis

ROI analysis of the fMRI activation elicited by the various adaptation conditions (SoSg, Same object/Same grasp; SoDg, Same object/Different grasp; DoSg, Different object/Same grasp; DoDg, Different object/Different grasp) as well the “Point” condition. Selection of the ROI voxels was based on both anatomical and functional criteria: object-related voxels were chosen individually in each subject if they were within the FuG and showed object-related adaptation (i.e., significantly higher activation for the condition “Different object/Same grasp” than for the condition “Same object/Same grasp” using single-subject GLM analysis, $p < 0.05$, corrected). Analogously, grasp-related voxels were chosen if they were within the aIPS and showed grasp-related adaptation (significantly higher activation for the “Same object/Different grasp” condition than for the “Same object/Same grasp” condition in each subject, $p < 0.05$, corrected). An example of the ROIs from one subject (subject #9) is shown in the insets. These include a ventral view of the inflated brain, showing the object-related areas in the FuG (encircled by cyan lines) and a dorsal view depicting the grasp-related areas in the aIPS. (Left and right panels) Bar histograms of the average percent signal change and hemodynamic response curves for the five conditions in the four ROIs: left aIPS ($n = 10$), right aIPS ($n = 8$), left FuG ($n = 9$), and right FuG ($n = 10$). Error bars denote SEM. Gray background denotes the time (onset to offset) of the condition.

between the two conditions (as such interaction exists in the SoSg condition, but not in the Point condition). In addition, our results in experiment I indicate that ventral areas are engaged in the representation of the objects, but they are not affected by the hand-object interaction. Thus, in the ventral ROI, the SoSg and Point conditions should generate similar activation (since in both conditions the subject repeatedly saw the same object).

Indeed, significant preference for the SoSg condition (compared to the Point condition) was found *only* in the grasp-related ROIs in the aIPS ($t = 2.63$, $p < 0.05$ in the right aIPS and $t = 4.78$, $p < 0.001$ in left aIPS).

Up to this point, we focused our attention on the aIPS and FuG, stressing the fact that the patterns of selective activation were remarkably consistent across experiments (i.e., contralateral representation preference, task-related activation, and adaptation). However, each one of the paradigms elicited activation in other visual areas, such as lateral occipital sulcus and dorsal occipital and parietal areas (see Figures 2, 4, and 7 and Tables 1 and 2), in which the picture seemed more complex. To gain further understanding of the specific characteristics of these intermediate areas, we chose the voxels showing a contralateral preference in experi-

ment I (in either direction, see Figure 2) as Talairach-based ROIs and assessed their fMRI activation in the two other paradigms. Table 3 summarizes the comparison between the exemplary ROIs (aIPS and FuG) and the intermediate ROIs (right and left dorsal occipital areas and right lateral occipital sulcus) across the three paradigms. In fact, in the dorsal occipital ROIs and the right lateral occipital sulcus ROI, we found mixed effects; those ROIs show significant preference for the representation of the contralateral hand as well as indications for object-based adaptation. This result is not entirely unexpected, since the information about the acting hand as well as the object manipulated (analyzed in the ventral stream) has to be conveyed to the dorsal pathway to allow preparation of the appropriate motor program.

Discussion

The goal of this study was to find clear evidence for dissociation between the putative involvement of dorsal and ventral visual areas, in action and object recognition, respectively. This was done by using three different fMRI-based display and analysis techniques:

Table 3. Summary of the Preference Properties of Cortical Areas across Experiments

ROI (Talairach Coordinates)	Task	Object Adaptation (p Value)	Grasp Adaptation (p Value)	Dominant Feature
Right fusiform gyrus (26, -56, -10)	Name	0.0001	N.S.	Rh/Lo
Left fusiform gyrus (-22, -58, -7)	Name	0.024	N.S.	Lh/Ro
Right dorsal occipital (14, -79, 34)	Count	N.S.	N.S.	Lh/Ro
Left dorsal occipital (-11, -79, 38)	Name	Marginal	N.S.	Rh/Lo
Right lateral occipital sulcus ("EBA") (43, -64, 6)	Count*	Marginal	N.S.	Lh/Ro
Right anterior IPS (32, -37, 55)	Count	N.S.	0.009	Lh/Ro
Left anterior IPS (-36, -42, 54)	Count	N.S.	0.009	Rh/Lo
Left pre-central sulcus (-27, -10, 58)	Count	N.S.	Marginal	Rh/Lo

This table summarizes the preference in the fMRI activation in the different experimental paradigms for ROIs that showed significant contralateral bias in experiment 1 (the list of areas is in the first column, see also Figure 2).

Task effect: task preference in each ROI. "Name": preference for the naming task ("name the object"). "Count": preference for the counting task ("count how many fingers interact with the object"). Significant task-dependent effects are denoted by an asterisk ($p < 0.05$).

Object and grasp adaptation effects: given in terms of the p values of a repeated-measures ANOVA for the object and grasp identity effects. N.S = $p > 0.1$. Marginal = $0.05 < p < 0.1$.

Dominant feature: the preferred clip in each ROI: "Rh/Lo": preference for "Right hand/Left object" clips. "Lh/Ro": preference for "Left hand/Right object" clips. Bold letters denote the preferred contralateral feature (hand or object).

contralateral representation, task-related activation, and fMRI adaptation. The converging evidence from *all* of *these* methods suggests the existence of at least two distinct brain areas that are engaged in processing different aspects of observed object manipulation—ventral areas, such as the FuG, that are likely to play a role in the processing of object identity, and dorsal areas, such as the vicinity of the intraparietal sulcus, and specifically aIPS, which is active during observation of object grasping movements. Before making this conclusion, we address the issue of possible confounding factors that potentially could have led us to the wrong conclusions.

Possible Confounding Factors

Cerebellar Activation

One issue that is of concern in the two experiments is that the group results activation in the ventral loci (for example in FuG) is possibly due to a cerebellar source of activation. Specifically, one may wonder (given the degree of variation in the exact location of the FuG across subjects), whether the ventral occipital activation (contralateral to the object's position) seen in the multisubject map (Figure 2; experiment I) may have resulted from a partial volume of activation originating in the cerebellum. The cerebellum is typically active during *ipsilateral* motor actions and somatosensory stimulation (Nitschke et al., 1996; Leicht and Schmidt, 1977). Thus, if there is also an *ipsilateral* representation of *observed actions* in the cerebellum, the resulting cerebellar activation would be *contralateral* to the *object's location* in our design. However, we think this explanation is unlikely for a number of reasons. First, the ipsilateral activation in the cerebellum is typically seen during motor and tactile tasks, while in our experiments the activation was a result of the visual input (since there was no somatosensory stimulation or motor output). Second, and more important, the group results (in experiment I) were verified in the *subject by subject* (ROI) analysis (Figure 3B). In this analysis, voxels were assigned to the ventral ROI only if they were within the cerebral cortex (which could be established unequivocally)

and if the most significant voxel within each cluster was also located in the cerebral cortex (see also Figure S2), showing that in each of the single subjects, the voxels displaying contralateral preference for objects in the ventral regions were located in the cerebral cortex.

Low-Level Visual Effects

Another worry is that the contralateral activation in ventral occipital areas (with respect to the object's visual hemifield) is a result of differences in low-level elements between the two hemifields that have nothing to do with object recognition (such as local contrast differences). Thus, ten different objects (with variable levels of luminance) were seen in the hemifield in which the objects were shown, whereas in the other hemifield the subjects observed the same hand making reaching movements toward the center of the screen. This explanation cannot be completely ruled out and may be relevant for the contralateral activation in the early visual areas of the occipital cortex (see Figure 2). However, the contralateral activation seen in the ventral areas extends beyond the border of the retinotopic areas (area V4 ventral, see Figure 2). Additionally, in the ROI analysis, we show that the contralateral preference can be seen in high-level visual areas—i.e., areas that show greater activation during observation of object manipulation clips than during observation of spatially scrambled versions of those clips—despite the fact that the difference in local contrast is greater in the spatially scrambled clips.

Sensitivity to Visual Motion

It may be argued that the reported dorsal activation in experiment I, which we associated with a preference for the representation of hand action, may be due to the observed *hand motion* or even simply the prevalence of motion per se in the contralateral side of the screen. This is unlikely to explain the whole picture, however, since hand motion cannot account for the grasping-dependent adaptation in aIPS, seen in experiment II, as similar hand movements were observed in all conditions, on the same side of the screen. Furthermore, in the Point condition of experiment II, subjects viewed clips of hand trajectories similar to the ones in the

grasping conditions, which generated little fMRI activation in the dorsal ROIs. Thus, the contralateral preference for the viewed hand action, seen in the dorsal areas (such as aIPS) in experiment I, probably represents preference for high-level visual components of the scene, such as the grasping movement (i.e., hand-object interaction) rather than visual motion per se.

The Hand as an Object

In experiment I, using the contralateral representation, we showed dissociation between the representation of the hand action (in the dorsal areas) and the objects (in the ventral ones). However, it may be claimed that the hand itself is an object. Why then do we observe a clear contralateral preference for the inanimate objects (as opposed to the hand) in the ventral occipitotemporal areas? One possible explanation is that viewing human body parts and inanimate objects generates distinct and spatially separate activation in the ventral occipital cortex. Indeed, recently Downing et al. (2001) have shown that a cortical region in the right lateral occipitotemporal cortex (termed “extrastriate body area” [EBA]) shows a greater response to images of body parts than to inanimate objects. This may also be observed in our results (see Figure 2). We found a preference for the “Left hand/Right object” over its mirror image, in the *right* lateral occipital sulcus (presumably because of selectivity to the presence of the contralateral *hand* rather than the ipsilateral nonanimate objects). This locus overlaps with the Talairach coordinates of EBA (see Figure 2). Note that this hand preference is opposite to the general *object* preference that is characteristic of the ventral occipitotemporal areas.

Numerical Judgment in the Parietal Cortex

In experiment 1, we found modulation of the fMRI activation in the aIPS and the FuG which was elicited by manipulation of the task. Specifically, when the subjects were asked to attend to the grasping movement (by counting how many fingers interact with the object) the activation in the aIPS was higher compared to the activation during performance of the object-oriented task (“Naming”). However, there is evidence to suggest that the IPS is involved in counting and numerosity judgments (Piazza et al., 2004). Hence, it is possible that the activation associated with the counting task (the action-oriented task) was related to counting rather than the attention to the grasping movement. Nevertheless, we find *selective* fMRI activation in the aIPS (i.e., preference for the contralateral hand) during the *naming* task as well as during the counting task. Similarly, the contralateral *object* preference in the FuG can be seen during *both* object naming and the counting task (see Figure 3B, showing the fMRI activation for the two sets of visual clips, under the two different tasks). These results indicate that the primary factor determining the pattern of activation is the nature of the visual input. Task-dependent modulation is clearly secondary in its importance, although it does have a significant effect (see also Figures 3–5). Moreover, while Piazza et al. emphasize the putative role of IPS in numerical judgments, the foci of activation during performance of such tasks is typically in the horizontal IPS (Talairach coordinates: X = -36, Y = -60, Z = 52 in the left hemisphere and 28, -56, 52 in the right hemisphere). Our foci of parietal activation (i.e., center of mass), showing

significant preference for the “count” task over the naming task, were located in the anterior part of the IPS (-37, -44, 50 in the left hemisphere, and 35, -48, 56 in the right). We therefore suggest that the activation in the counting task was more likely to be due to focused attention on the interaction between the grasping hand and the grasped object, rather than counting per se.

Internal Representation of Observed Actions in aIPS

We show in this study that dorsal stream areas are active during observation of actions on objects, in the absence of movement, or preparation for movement by the subjects.

The “direct matching hypothesis” (Rizzolatti et al., 2001) maintains that one recognizes action performed by others by generating an internal representation of the observed action, as if one was executing the observed action. This hypothesis is supported by the discovery of “mirror neurons” in area F5 in the monkey’s frontal lobe and in the inferior parietal lobule (Rizzolatti et al., 1996; Fogassi et al., 2005). These neurons are active during the execution of goal-directed actions, such as grasping, and critically, they are also active during observation of another monkey, or the experimenter, doing the same or similar actions.

Converging data from neuropsychological, behavioral, and imaging studies propose the existence of a mirror system in humans too. Aziz-Zadeh et al. (2002) showed that motor-evoked potentials are higher when applying transcranial magnetic stimulation (TMS) to the motor cortex during action observation than in the absence of such viewing. Using fMRI, Buccino et al. (2004) have shown that the inferior parietal lobule and the inferior frontal gyrus are active during mere observation of an external action (guitar playing). Motor-related activation in those areas has been documented in imaging studies as well as in single-unit recording in monkeys (Culham et al., 2003; Shikata et al., 2003). Culham et al. have shown that the aIPS is more active during execution of grasping than during execution of reaching movements. Our results are congruent with the direct matching hypothesis; we show robust activation in the aIPS during *observation* of object manipulation clips. Specifically, *observation* of object grasping (as opposed to mere pointing) led to activation in the aIPS, bilaterally, similar to that evoked by *execution* of grasping movement previously reported (Culham et al., 2003). This supports the claim that aIPS may be engaged in the internal representation of observed actions.

The Nature of the Internal Representation in aIPS

In experiment I, we have shown contralateral preference in the aIPS with respect to the location of the hand. But was this activation due to the fact that subjects viewed the right *hand* or was it because the (right) hand was mainly on the *right side of the screen* (or visual field). Similarly, in the mirror condition, the left *hand*, manipulating the objects, was located mainly on the *left side* of the screen. Hence, the contralateral preference in the aIPS could be a result of two different frames of external action representation:

1. Contralateral *visual field* representation: Activation is due to contralateral preference for the hand action in terms of its *retinotopic* location (for example, activation in the *right* hemisphere when the hand is seen on the *left* side of the screen). Such a representation in the parietal cortex is supported by various neurophysiological studies in monkeys (Mountcastle et al., 1981).
2. Internal motor representation: The “direct matching hypothesis” claims that when we observe action made by others, an internal motor representation of this action is built automatically in our motor system. Taking this hypothesis one step further, it could be possible that observation of *right* hand actions will induce higher activation in the *left* hemisphere, and observation of left hand actions will induce higher activation in the right motor system of the observer, *irrespective the location of the observed actions in the visual field*.

Support for the latter hypothesis can be seen in the fact that in experiment I, although most of the hand action was seen in one side of the screen, the interaction between the hand and the object usually took place at the opposite side of the screen (in the object side of the screen). Thus, it seems that the more relevant parameter governing the activation in aIPS may be the hand *identity* rather than its position in the visual field. However, further research is needed in order to identify the frame of external action representation in the aIPS.

Segregation and Integration of Visual Information

Until this point, we stressed the results supporting the hypothesis of a functional dissociation between the ventral and dorsal streams during object and action recognition. However, this is clearly a simplified view. The acting hand has to be identified in the ventral stream before its actions could be matched to an internal motor program in the parietal lobe. Therefore, a complete distinction between action and object recognition is probably artificial. In fact, indications for convergence of information regarding both object identity and the nature of the action can be seen in our study in the left aIPS. In this ROI, we found contralateral representation for the location of the hand in experiment I and grasp-based adaptation in experiment II. Nevertheless, this ROI displayed object-based adaptation as well. This result is consistent with single-cell recordings in the monkey's AIP showing neural discharge for the mere observation of graspable objects (Murata et al., 1997). It seems therefore that the representation of hand action in the aIPS is not completely distinct from the representation of the goal of the action—i.e., the object. Furthermore, recent single-cell recordings in the monkey's inferior parietal lobule (IPL) suggest that, besides the representation of hand actions and the manipulated objects, some neurons in IPL may even be involved in the coding of the inferred *intention* of the observed experimenter (Fogassi et al., 2005).

Another approach to investigate the confluence of the two processes is through analysis of the activation in intermediate regions along the pathways, such as the

lateral occipital sulcus and the dorsal occipital regions (i.e., dorsal BA 19). For example, in experiment I, we found contralateral representation of the *hand action* in the lateral occipital sulcus and in dorsal occipital loci. Even so, in experiment II, we found indications for *object*-based adaptation in the same ROIs (Figures 7 and 8; Figure S1). This convergence of effects may underlie dorsal-ventral integration processes, such as those seen in the superior temporal cortex (for review, see Karnath, 2001); however, this speculation should be further explored.

Conclusions

In this study, we show direct evidence from three different methodologies for an overall functional dissociation between the representation of viewed hand actions and objects in dorsal and ventral visual areas, respectively. The results suggest that, in addition to the well established involvement of the dorsal system (and specifically the aIPS) in action planning and execution; it is involved in action recognition. The congruency between motor and visual properties in the same loci of the parietal cortex support the visuomotor characteristics attributed to those areas and suggests that the parietal cortex plays a role in visual recognition of actions made by others.

Experimental Procedures

MRI Subjects

Eleven volunteers without histories of neurological, psychiatric, or visual deficits (6 women and 5 men, aged 25–45) participated in the present experiments. The Tel-Aviv Sourasky Medical Center Ethics Committee approved the experimental procedure. Written informed consent was obtained from each subject.

MRI Acquisition

The BOLD fMRI measurements were performed in a whole-body 1.5-T, Signa Horizon, LX8.25 General Electric scanner. The functional MRI protocols were based on a multislice gradient echo-planar imaging and a standard head coil. The functional data were obtained under the optimal timing parameters: TR = 3 s, TE = 55 ms, flip angle = 90°, imaging matrix = 80 × 80, FOV = 24 cm. The 27 slices with slice thickness 4 mm (with no gap) were oriented in the axial position. The scan covered the whole brain. The fMRI images were superimposed on T1-weighted 3D SPGR images (voxel size = 1 × 1 × 1 mm³) that were recorded after the second experimental run.

Experimental Setup

Footages were taken using a digital camera (Sony trv60e), edited on a PC (using the program “Windows Movie Maker”) and back-projected via an LCD projector (Epson MP 7200, Japan) onto a tangent screen located inside the scanner in front of the subject. Subjects viewed the screen through a tilted mirror.

Visual Stimuli

Experiment I

A set of 16 object manipulation clips and a visual control clip, each 12 s long, were shown in this experiment. The “Right hand/Left object” clips were composed of ten 900–1500 ms black and white footages of a right hand approaching from the right side of the screen, grasping and releasing an object (total time = 12 s). The footages were taken using a set of 15 manmade graspable objects, such as different jars, cups, scissors, etc. Six to ten footages were taken with each object, showing different grasping movements. Each clip was composed of ten footages of different objects. The “Left hand/Right object” clips were generated by a “flip horizontal” operation on the “Right hand/Left object” footages. In all of the

clips, the objects did not move throughout the grasping movements. The same two sets of clips were shown twice: once while the subjects performed an object-oriented task, covertly naming the objects ("Name"), and once during performance of an action oriented task, covertly counting how many fingers interact with the object ("Count").

In the control "scramble" condition, a 12 s object manipulation clip was decomposed to frames (24 frames a second), every frame was spatially scrambled (36 × 24 fragments in each frame, ensuring that the hand and the objects could no longer be identified), and then the frames were recomposed to a 12 s clip. A fixation point appeared in the middle of the screen throughout the experiment. The images in all clips subtended 22 × 22 degrees.

Experiment II

The visual stimuli were composed of the same "Right hand/Left object" footages used in experiment I. Each clip was composed of ten footages, showing either (1) the same footage repeatedly, termed "Same object/Same grasping" (or SoSg), (2) different grasping of the same object (SoDg), (3) the same grasping of different objects (DoSg), and finally, (4) different grasping of different objects (DoDg). The fifth condition was composed of ten identical pointing movements toward the same object (termed Pointing). As in experiment I, a fixation point appeared in the middle of the screen throughout the experiment.

Experimental Paradigm

The experiments were carried out using a block design format. Five blocks were interleaved and were repeated four times with different stimuli in a counterbalanced manner. Each block lasted 12 s and was followed by a rest period of 9 s, in which the subjects maintained fixation on a blank screen. The first and last rest periods were longer (27 and 15 s, respectively). In experiment I, visual instructions concerning the next epoch were shown for 500 ms at the end of each rest period. Subjects were briefly trained before the experiment to verify that they are able to maintain fixation and respond to the instructions properly.

Data Analysis

Data analysis was performed using the BrainVoyager 4.96 and BrainVoyager Qx software package (Brain Innovation, Maastricht, The Netherlands, 2000). The functional images were superimposed on two-dimensional anatomical images and incorporated into the three-dimensional data sets through trilinear interpolation. Before statistical analysis, raw data were examined for motion and signal artifacts. Head motion correction and high-pass temporal filtering in the frequency domain (3 cycles/total scan time) were applied in order to remove drifts and to improve the signal-to-noise ratio. The complete data set was transformed into Talairach space, Z-normalized, and concatenated. General linear model (GLM) approach was used to generate statistical parametric maps; the hemodynamic response function was modeled using standard parameters (Boynton et al., 1996). Significance levels were calculated, taking into account the probability of a false detection for any given cluster (Forman et al., 1995), based on Monte Carlo simulation (AlphaSim by B. Douglas Ward, a software module in Cox [1996]).

The activation time course of individual subjects was obtained from statistically significant clusters in each region of interest (ROI) by applying the GLM analysis. The average percent signal change (from 9 to 15 s after the onset of the condition) was calculated for each subject and then averaged across subjects. Paired two-tailed t test was applied in order to show significant differences between the conditions. Voxels were identified as being in the Fusiform Gyrus (FuG) or the aIPS on an individual basis, using anatomical markers—the fusiform gyrus in the ventral stream and the anterior part of the intraparietal sulcus in the dorsal stream, respectively.

Across-subjects statistical parametric maps (Figures 2, 4, and 7) were calculated using hierarchical random-effects model analysis (Friston et al., 1999). The retinotopic borders displayed on the Talairach-normalized brain were estimated using the rotating wedge technique (Sereno et al., 1995) in one of the subjects (subject #1). The approximate retinotopic borders were assessed using the phase information. The statistical parametric maps were overlaid on a cortical surface map of a representative subject (#1). The surface maps were reconstructed from the T1-weighted 3D SPGR

scan. The procedure included segmentation of the white matter using a grow-region function, the smooth covering of a sphere around the segmented region, and the expansion of the reconstructed white matter into the gray matter. The surface was then unfolded, cut along the calcarine sulcus, and flattened.

Supplemental Data

The Supplemental Data for this article can be found online at <http://www.neuron.org/cgi/content/full/47/3/457/DC1>.

Acknowledgments

We thank A. Stark, T. Orlov, T. Makin, and A. McKayton for insightful comments; T. Orlov for the help with the 3D cortex reconstructions; and Y. Shalitin for his assistance in the cover design. This study was funded by the Israel Science foundation of the Israel Academy of Sciences grant # 80009 and the Mcdonell-Pew foundation grant # 220020046.

Received: February 2, 2005

Revised: May 16, 2005

Accepted: June 29, 2005

Published: August 3, 2005

References

- Aglioti, S., DeSouza, J.F., and Goodale, M.A. (1995). Size-contrast illusions deceive the eye but not the hand. *Curr. Biol.* 5, 679–685.
- Aziz-Zadeh, L., Maeda, F., Zaidel, E., Mazziotta, J., and Iacoboni, M. (2002). Lateralization in motor facilitation during action observation: a TMS study. *Exp. Brain Res.* 144, 127–131.
- Boynton, G.M., Engel, S.A., Glover, G.H., and Heeger, D.J. (1996). Linear systems analysis of functional magnetic resonance imaging in human V1. *J. Neurosci.* 16, 4207–4221.
- Buccino, G., Vogt, S., Ritzl, A., Fink, G.R., Zilles, K., Freund, H.J., and Rizzolatti, G. (2004). Neural circuits underlying imitation learning of hand actions: an event-related fMRI study. *Neuron* 42, 323–334.
- Culham, J.C., Danckert, S.L., DeSouza, J.F., Gati, J.S., Menon, R.S., and Goodale, M.A. (2003). Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. *Exp. Brain Res.* 153, 180–189.
- Downing, P.E., Jiang, Y., Shuman, M., and Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science* 293, 2470–2473.
- Fogassi, L., Ferrari, P.F., Gesierich, B., Rozzi, S., Chersi, F., and Rizzolatti, G. (2005). Parietal lobe: from action organization to intention understanding. *Science* 308, 662–667.
- Forman, S.D., Cohen, J.D., Fitzgerald, M., Eddy, W.F., Mintun, M.A., and Noll, D.C. (1995). Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): use of a cluster-size threshold. *Magn. Reson. Med.* 33, 636–647.
- Friston, K.J., Holmes, A.P., and Worsley, K.J. (1999). How many subjects constitute a study? *Neuroimage* 10, 1–5.
- Goodale, M.A., and Milner, D. (1992). Separate visual pathways for perception and action. *Trends Neurosci.* 15, 20–25.
- Goodale, M.A., Meenan, J.P., Bulthoff, H.H., Nicolle, D.A., Murphy, K.J., and Racicot, C.I. (1994). Separate neural pathways for the visual analysis of object shape in perception and prehension. *Curr. Biol.* 4, 604–610.
- Grill-Spector, K., and Malach, R. (2001). fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychol. (Amst.)* 107, 293–321.
- James, T.W., Humphrey, G.K., Gati, J.S., Menon, R.S., and Goodale, M.A. (2002). Differential effects of viewpoint on object-driven activation in dorsal and ventral streams. *Neuron* 35, 793–801.
- James, T.W., Culham, J., Humphrey, G.K., Milner, A.D., and Goodale, M.A. (2003). Ventral occipital lesions impair object recognition

but not object-directed grasping: an fMRI study. *Brain* 126, 2463–2475.

Karnath, H.O. (2001). New insights into the functions of the superior temporal cortex. *Nat. Rev. Neurosci.* 2, 568–576.

Leicht, R., and Schmidt, R.F. (1977). Somatotopic studies on the vermal cortex of the cerebellar anterior lobe of unanaesthetized cats. *Exp. Brain Res.* 27, 479–490.

Livingstone, M., and Hubel, D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science* 240, 740–749.

Mishkin, M., and Ungerleider, L.G. (1982). Contribution of striate inputs to the visuospatial functions of parieto-preoccipital cortex in monkeys. *Behav. Brain Res.* 6, 57–77.

Mountcastle, V.B., Andersen, R.A., and Motter, B.C. (1981). The influence of attentive fixation upon the excitability of the light-sensitive neurons of the posterior parietal cortex. *J. Neurosci.* 1, 1218–1225.

Murata, L., Fadiga, L., Fogassi, V., Gallese, V., Raos, V., and Rizzolatti, G. (1997). Object representation in the ventral premotor cortex (area F5) of the monkey. *J. Neurophysiol.* 78, 2226–2230.

Niemeier, M., Goltz, H.C., Kuchinad, A., Tweed, D.B., and Vilis, T. (2005). A contralateral preference in the lateral occipital area: sensory and attentional mechanisms. *Cereb. Cortex.* 15, 325–331.

Nitschke, M.F., Kleinschmidt, A., Wessel, K., and Frahm, J. (1996). Somatotopic motor representation in the human anterior cerebellum. A high-resolution functional MRI study. *Brain* 119, 1023–1029.

Piazza, M., Izard, V., Pinel, P., Le Bihan, D., and Dehaene, S. (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron* 44, 547–555.

Rizzolatti, G., Fadiga, L., Gallese, V., and Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Brain Res. Cogn. Brain Res.* 3, 131–141.

Rizzolatti, G., Fogassi, L., and Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat. Rev. Neurosci.* 2, 661–670.

Sereno, M.I., Dale, A.M., Reppas, J.B., Kwong, K.K., Belliveau, J.W., Brady, T.J., Rosen, B.R., and Tootell, R.B. (1995). Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science* 268, 889–893.

Shikata, E., Hamzei, F., Glauche, V., Koch, M., Weiller, C., Binkofski, F., and Buchel, C. (2003). Functional properties and interaction of the anterior and posterior intraparietal areas in humans. *Eur. J. Neurosci.* 17, 1105–1110.

Tusa, R.J., Rosenquist, A.C., and Palmer, L.A. (1979). Retinotopic organization of areas 18 and 19 in the cat. *J. Comp. Neurol.* 185, 657–678.