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Differential Effects of Viewpoint on Object-Driven Activation in Dorsal and Ventral Streams

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Summary

Using fMRI, we showed that an area in the ventral temporo-occipital cortex (area vTO), which is part of the human homolog of the ventral stream of visual processing, exhibited priming for both identical and depth-rotated images of objects. This pattern of activation in area vTO corresponded to performance in a behavioral matching task. An area in the caudal part of the intraparietal sulcus (area cIPS) also showed priming, but only with identical images of objects. This dorsal-stream area treated rotated images as new objects. The difference in the pattern of priming-related activation in the two areas may reflect the respective roles of the ventral and dorsal streams in object recognition and object-directed action.

Introduction

Neuroimaging studies have consistently shown that the ventral visual cortex, and in particular the lateral occipital complex (LOC), is highly active during object recognition (Corbetta et al., 1991; Dale et al., 2000; Faillenot et al., 1997; Grill-Spector et al., 2000; Halgren et al., 1999; James et al., 2000; Kanwisher et al., 1996; Kraut et al., 1997; Malach et al., 1995; Price et al., 1996; Sergent et al., 1992). In some of these studies (Dale et al., 2000; Faillenot et al., 1997; Grill-Spector et al., 2000; James et al., 2000; Kraut et al., 1997), activation has also been found in the posterior parietal cortex during object recognition tasks, specifically in the caudal part of the intraparietal sulcus (cIPS). The activation in both of these regions (LOC and cIPS) is modulated by previous visual experience with objects (for example, see Badgaiyan, 2000; Buckner et al., 1998; Dale et al., 2000; James et al., 2000; Jiang et al., 2000; Squire et al., 1992; van Turennout et al., 2000; Vuilleumier et al., 2002; for review, see Cabeza and Nyberg, 2000; Schacter and Buckner, 1998; Wiggs and Martin, 1998). This modulation, which is a reduction in activation, is believed to reflect a behavioral "priming" effect in which subjects respond more quickly and/or more accurately to objects they have seen before.

Area LOC is generally thought to be part of the object recognition network within the human homolog of the monkey ventral stream (Malach et al., 1995). It has been suggested that this stream of visual processing plays the most important role in the long-term representation and categorization of objects in the visual world. But what about the object-related activation that has been found in area cIPS? It has been suggested that this region of the posterior parietal cortex might be part of a human homolog of the monkey dorsal stream (Culham and Kanwisher, 2001). One function of the dorsal stream appears to be the visual control of skilled actions, such as object-directed grasping movements (Goodale and Milner, 1992). Therefore, the activation seen in area cIPS may reflect some sort of object processing that is related to action (Faillenot et al., 1997; Shikata et al., 2001). Thus, it is possible that the patterns of activation seen in areas LOC and cIPS reflect fundamentally different processes, one related to object perception, the other to object-directed actions. If this is the case, then the effects of priming on activation in areas LOC and cIPS might also be different, and could mirror the effects that have been shown to occur in object recognition and the visual control of action.

In everyday life, we are able to recognize objects we have seen before even when we encounter them from a different viewpoint. There is considerable debate in the literature, however, as to how this occurs and whether object representations are viewpoint dependent or not (for review, see Jolicoeur and Humphrey, 1998; Tarr and Bulthoff, 1998; Wallis and Bulthoff, 1999). Nevertheless, most studies have shown that previous exposure to an object will facilitate recognition to some extent, even when the object is presented from a different viewpoint (for example, see Biederman and Gerhardstein, 1993; Williams and Tarr, 1999). In short, perceptual priming shows evidence for some generalization across viewpoints.

Although successful object recognition demands generalization across many different viewpoints, this is not true for object-directed actions such as grasping. Here the orientation of the object with respect to the actor is critical. The same goal object seen from different vantage points could demand quite different hand postures. The little experimental evidence that exists on this point has found that "action priming" is indeed orientation specific (Craighero et al., 1996).

Given these differences in the effects of object viewpoint on perceptual and action priming, one might then expect to see corresponding differences in the patterns of activation with priming in areas LOC and cIPS. Because area LOC is part of the ventral "perception" pathway, the effects of priming on activation should show more generalization across viewpoints. In contrast, because area cIPS is part of the dorsal "action" pathway, the effects of priming should not generalize across changes in viewpoint when the change would cause the object to be acted upon differently. We examined this possibility by measuring brain activation in subjects while they were presented with images of three-dimensional objects in two experiments (Experiments 2 and 3). In both experiments, the first presentation of each object was at a set viewing angle, but when the subjects were re-presented with the objects, each object was

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shown either at the identical view or at a different view. An initial behavioral experiment (Experiment 1) demonstrated that the changes in viewpoint that were used in Experiments 2 and 3 did not produce a cost in terms of the time to match two objects. The viewpoint change was designed to not foreshorten the axis of elongation of the objects, and to limit self-occlusion of object parts.

To examine the generality of any differences that we found between the ventral and dorsal object areas, in Experiment 2 we used both common and novel objects (Figure 1). The use of these two object types was prompted by a study suggesting that priming of common and novel objects might produce different results (Henson et al., 2000). In Experiment 2, we found an unexpected order effect that indicated a possible adaptation to object orientation, in addition to the main priming effect based on object identity. Experiment 3 was designed to control for the order effect, but at the same time allowed us to evaluate the magnitude of the possible adaptation to orientation that occurred in Experiment 2. Experiment 3 used only common objects because there were no differences in the pattern of activation produced by the common and novel objects in Experiment 2.

Results

Experiment 1 was a purely behavioral experiment that was designed to evaluate the effects of the viewpoint change used in Experiments 2 and 3. Subjects ($n = 19$) performed a sequential matching task on pairs of objects that were presented in either the same or different views. Examples of the changes in viewpoint are shown in Figure 1A. Only the common objects were used in this experiment. As Figure 1B illustrates, there were no significant differences in response time or accuracy between identical and rotated views of the objects for the sequential matching task. ($t_{(18)} = 0.87$, ns; $t_{(18)} = 0.81$, ns).

Experiments 2 and 3 used two separate groups of subjects ($n = 8$ and $n = 6$). In both experiments, subjects viewed both intact objects and scrambled versions of those same objects. Object-selective regions of the brain were localized separately for each experiment by comparing the activation produced while viewing intact objects with the activation produced while viewing scrambled objects (Figures 2 and 3). The region of occipital cortex that produced more activation to intact than scrambled objects is illustrated best in the ventral views of the brain shown in Figures 2 and 3. This large ventral occipito-temporal region has been termed the lateral occipital complex (LOC) (Grill-Spector et al., 2000; Malach et al., 1995) and consists of several functionally distinct sub-regions (Grill-Spector et al., 1998). Thus, because the LOC is thought to be functionally heterogeneous, we defined a region of interest (ROI) within the LOC that was relatively small but was highly correlated with the presentation of intact objects. We reasoned that a small and highly active ROI would be less likely to include more than one functionally distinct region.

We defined our ventral ROI as a 350 mm^2 area of cortical surface surrounding the focus of highest statistical reliability within the LOC from the grouped data (separately for each experiment). This ROI fell on the temporal-occipital boundary of the fusiform gyrus and was thus termed the ventral temporal-occipital area (vTO). There was also a region of parietal cortex that produced more activation to intact than scrambled objects, and it is illustrated best in the dorsal views of the brain shown in Figures 2 and 3. We defined a dorsal ROI as a 350 mm^2 area of cortical surface surrounding the focus of highest statistical reliability within the posterior parietal cortex, again from the grouped data, separately for each experiment. As was the case in previous studies of object-selective activation within the parietal cortex (Dale et al., 2000; Faillenot et al., 1997; Grill-Spector et al., 2000; James et al., 2000; Kraut et al., 1997), this region was within the caudal part of the intraparietal sulcus (cIPS). It should be noted that the position of area vTO in Experiment 2 was 1.4 cm anterior to its position in Experiment 3, not a negligible difference. This effect seems to be entirely due to individual differences between the subjects used in Experiments 2 and 3 and possibly exaggerated by the use of a fixed-effects statistical design.

Having defined two regions of interest for each experiment, we then measured the effect of viewpoint on priming-related changes in activation across these ROIs. These data are summarized in Figure 4 and presented in detail in Figure 5. Data represent right hemisphere activation, which was not significantly different from left hemisphere activation. Figure 4A shows the activation produced by the rotated primed views as a percentage of the initial (new) presentation of each object, using the activation produced by the identical primed views as a baseline. This measure reflects the amount of viewpoint specificity exhibited by a region. In area cIPS, the percentages are high, indicating that the activation with rotated objects in this region is similar in magnitude to the activation with the new objects. In area vTO, however, the percentages are low, indicating that the activation with rotated objects in this region is similar in magnitude to the activation with the identical objects.

The design of Experiment 3 was more robust than that of Experiment 2, because the order of the rotated and identical repeated conditions was counterbalanced and because all of the relevant conditions were collected within the same functional run. As Figure 4C shows, order effects that were present in Experiment 2 were greatly diminished in Experiment 3, such that they could not be contributing to the hypothesized priming effects. For Experiment 3, both areas vTO and cIPS showed significant priming effects, with the initial presentation of the objects producing more activation than later presentations of *identical* views of the objects ($t_{(5)} = 2.95$, $p < 0.05$; $t_{(5)} = 2.78$, $p < 0.05$). In contrast, area vTO, but not area cIPS, showed a reduction in activation when *rotated* images of the objects were presented ($t_{(5)} = 2.38$, $p < 0.05$). In fact, the later presentation of the rotated views produced significantly more activation than the later presentation of the identical views in area cIPS ($t_{(5)} = 2.39$, $p < 0.05$), but not in area vTO. Although Experiment 2 used a less robust design than Experiment 3, the pattern of results in Experiment 2 was the same as that of Experiment 3 (Table 1). This is further demonstrated by the results of a three-way analysis of variance that showed a significant interaction between priming

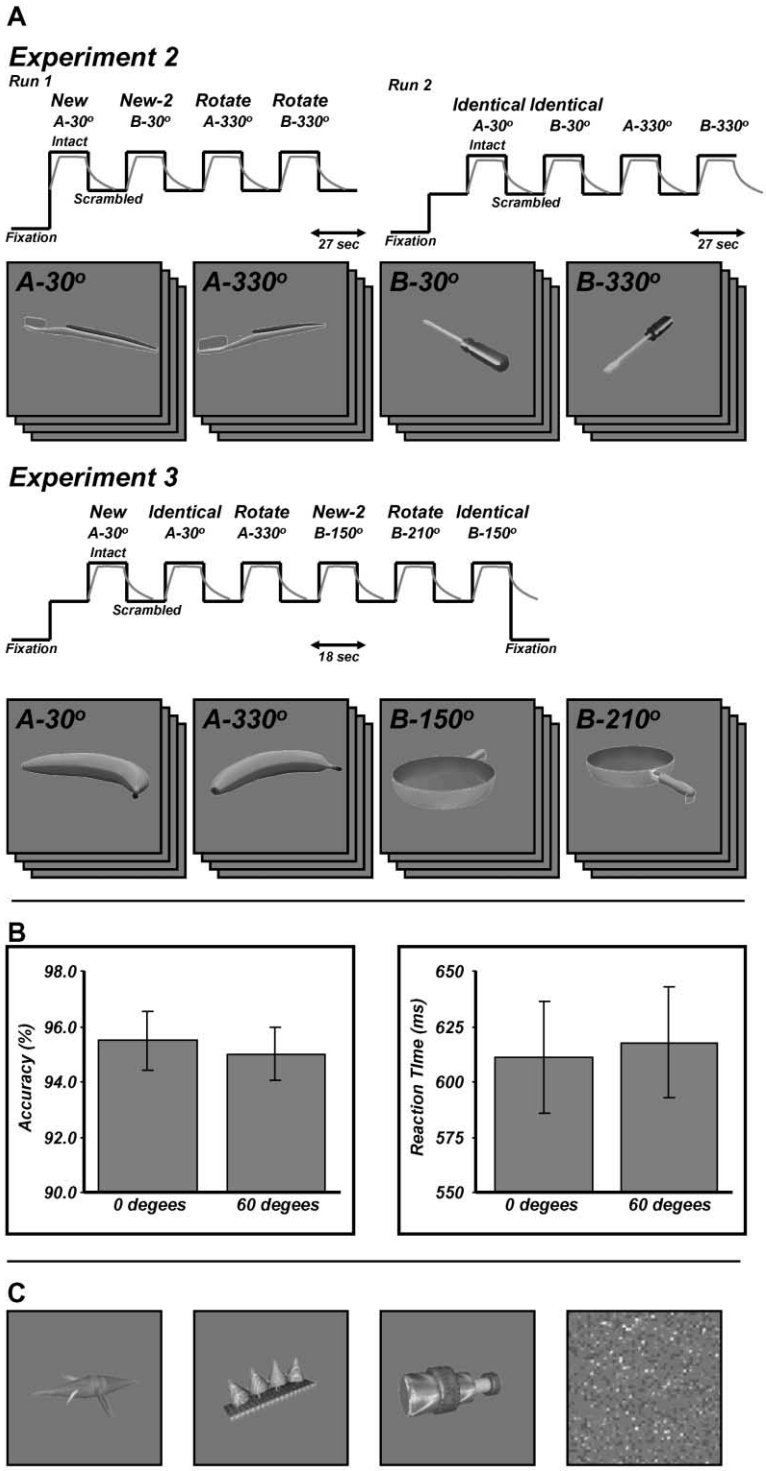

Figure 1. Stimuli and Imaging Protocols

(A) In Experiment 2, images of objects were presented to subjects in two separate runs. Each run began with 27 s of fixation and was followed by stimulus presentation blocks of 12 stimuli each. These stimulus blocks alternated between presenting intact objects and scrambled objects. The 12 objects that were presented in the first intact object block (A-30°) of a run were different from the 12 objects presented during the second intact object block (B-30°). The objects that were presented during the third and fourth intact object blocks (A-330°, B-330°) were the same objects that were presented in the first and second intact object blocks (A-30°, B-30°), but were rotated 60° in depth. Every stimulus was presented for 2.25 s, resulting in a total presentation time of 27 s for each entire block. The sets of objects that were presented in the second run were identical to those presented in the first run. In Experiment 3, images of objects were presented to subjects in a single run. It began and ended with 18 s of fixation; between which, there were stimulus presentation blocks of 12 stimuli each. These stimulus blocks alternated between presenting intact objects and scrambled objects. The 12 objects that were presented in the first intact object block (A-30°) of a run were different from the 12 objects presented during the fourth intact object block (B-150°). The objects that were presented during the third and fifth intact object blocks (A-330°, B-210°) were the same objects that were presented in the first and fourth intact object blocks (A-30°, B-150°), but were rotated 60° in depth. The images that were presented during the second and sixth intact object blocks (A-30°, B-150°) were the identical images that were presented in the first and fourth intact object blocks. Every stimulus was presented for 1.5 s, resulting in a total presentation time of 18 s for each block. Gray lines are modeled hemodynamic response functions used to create the predictor functions that were used to analyze the data.

(B) Data are from the sequential matching task used in Experiment 1. Only the 30° and 330° views were used; thus, 0° indicates objects presented at the same view, and 60° indicates objects presented at different views. Error bars represent the square root of the mean square error from the multivariate analysis of variance divided by the error degrees of freedom (sqrt[MSE/dfE]).

(C) Three examples of the novel objects used in Experiment 2 and one example of the scrambled objects used in Experiments 2 and 3.

condition and ROI ($F_{(2,11)} = 4.21$, $p < 0.05$), with no interactions between experiment and ROI ($F_{(1,12)} = 3.03$, ns), and no three-way interaction ($F_{(2,11)} = 0.54$, ns). There was a nonsignificant trend for an interaction between experiment and condition ($F_{(2,11)} = 3.15$, $p < 0.10$), but this was most likely due to the different stimulus presentation protocols used in the two experiments (Figure 1A), which appears to have caused an attenuation of all priming effects in Experiment 3.

Figure 4B shows the percentage activation produced by rotated objects for a larger ROI that includes all of the LOC. Including data from the whole LOC allows a comparison with studies that have used the entire LOC as a region of interest. The location of this ROI is indicated in Figure 3 by the dotted black outline. The activation produced in this ROI with the rotated objects fell between the pattern of activation produced by areas VTO and cIPS (Figure 4B).

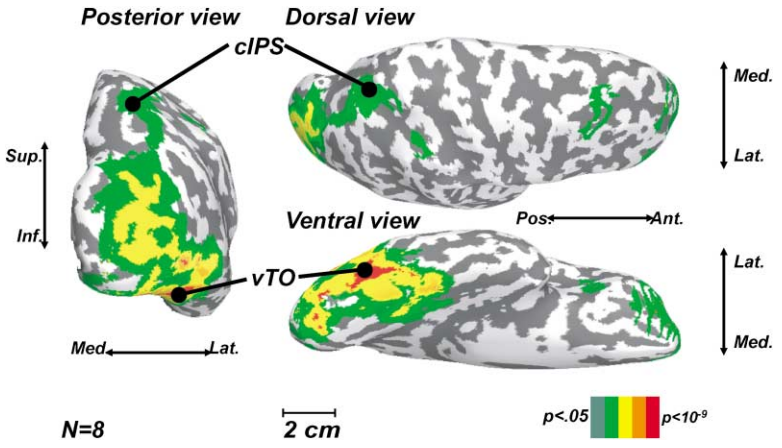

Figure 2. Results of Experiment 2

Brains are "inflated" to show activation within the sulci. Gyri appear in light gray and sulci appear in dark gray. Posterior, dorsal, and ventral views of only the right hemisphere are shown, but activation in the left hemisphere was similar. The activation map was generated from the data of eight subjects. All activated regions showed higher activation with intact than with scrambled objects. The lateral occipital complex (vTO) (Talairach coordinates: RH, $x = 43$, $y = -55$, $z = -24$; LH, $x = -37$, $y = -50$, $z = -24$) is indicated on the posterior and ventral views. The caudal part of the intraparietal sulcus (cIPS) (Talairach coordinates: RH, $x = 32$, $y = -69$, $z = 45$; LH, $x = -29$, $y = -68$, $z = 45$) is indicated on the posterior and dorsal views. The vTO and cIPS ROIs each included an area of cortical surface that was approximately 350 mm^2. Significance levels are uncorrected.

In Experiment 2, both novel and common objects were used. The novel objects were not used in Experiment 3 because, in Experiment 2, they produced the same basic pattern of activation as the common objects (Figure 5); that is, there were no interactions between familiarity and either priming condition ($F_{(2,6)} = 2.17$, ns) or ROI ($F_{(1,7)} = 2.25$, ns), and no three-way interaction ($F_{(2,6)} = 0.74$, ns).

As Figure 1A illustrates, two subsets of objects (A and B) were used in Experiments 2 and 3. In Experiment 2, images from these two object sets were presented at the same two viewpoints (30° and 330°). In Experiment 3, images from the two object sets were presented at different viewpoints (set A, 30° and 330°; set B, 150° and 210°). This difference in the protocols of Experiments 2 and 3 allowed us to evaluate the magnitude of the apparent adaptation to orientation (independent of object identity) that occurred in Experiment 2. Figure 4C shows the mean difference in activation for both experiments between the initial presentation of object set A and the initial presentation of object set B, where object set B was always the set of objects that was presented second. In other words, the vertical axis in Figure 4C measures the size of any order effects that were present in the activation produced in the two regions for the two experiments. There was an order effect in Experiment 2, such that the initial presentation of object set B resulted in significantly lower activation than the initial presentation of object set A in area cIPS ($t_{(7)} = 2.72$, $p < 0.05$), but not in area vTO ($t_{(7)} = 1.25$, ns). Despite this difference, however, there was only a nonsignificant trend for the order effect for area cIPS to be larger than for area vTO ($t_{(7)} = 2.09$, $p < 0.10$). There were no significant order effects in Experiment 3 in which the orientation of the test objects was changed between object set A and object set B.

Discussion

When subjects viewed objects that had been previously presented to them, the vTO an object-selective region in the ventral stream and part of the LOC, showed the same reduction in activation with rotated images of those objects as it showed with identical images. In other words, the observed priming effects on activity in area vTO were invariant with respect to these rotations in depth. This was not true for area cIPS, a region in the putative human homolog of the dorsal stream. Object-related activation in this posterior parietal region was reduced only when identical images were presented to the subject. That is, rotated images were treated as new objects.

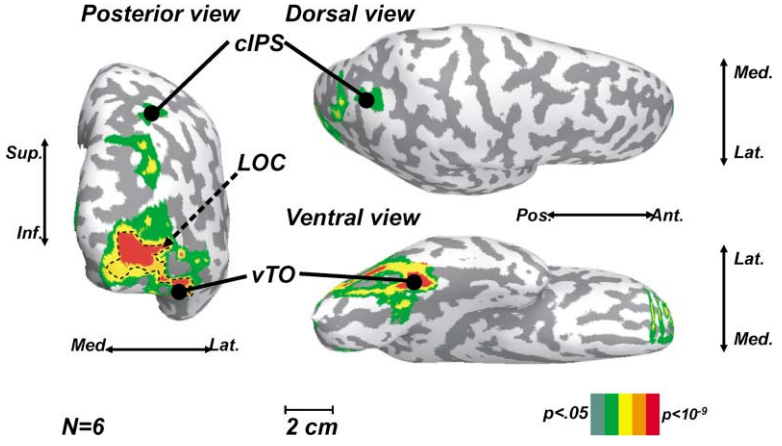

Figure 3. Results of Experiment 3

The activation map was generated from the data of six subjects. All activated regions showed higher activation with intact than with scrambled objects. The vTO (Talairach coordinates: RH, $x = 34$, $y = -43$, $z = -19$; LH, $x = -34$, $y = -46$, $z = -22$) is indicated on the posterior and ventral views. The cIPS (Talairach coordinates: RH, $x = 25$, $y = -74$, $z = 35$; LH, $x = -13$, $y = -72$, $z = 38$) is indicated on the posterior and dorsal views. The vTO and cIPS ROIs each included an area of cortical surface that was approximately 350 mm^2. The region that is outlined by the dotted black line is the lateral occipital complex (LOC). Significance levels are uncorrected.

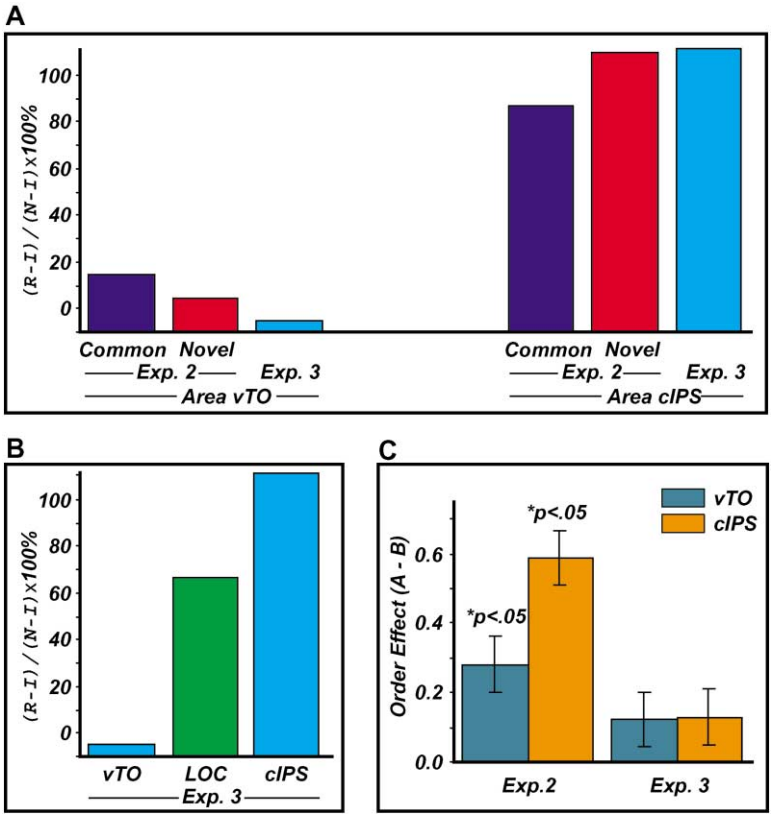

Figure 4. Priming Ratios and Order Effects

(A) The vertical axis indicates the amount of activation produced while viewing the repeated rotated objects (R), expressed as a percentage of the activation produced while viewing the initial presentation (N), using the activation during viewing of identical repeated objects (I) as the zero percent mark. A high value indicates that activation for the rotated objects was close to that of the initial presentation, whereas a low value indicates that activation for the rotated objects was close to that of the identical repeated presentation. Data are presented from both Experiments 2 and 3 ($n = 8$ and $n = 6$), for the vTO and cIPS ROIs. Data represent right hemisphere activation, which was not significantly different from left hemisphere activation. For Experiment 2, data from the common and novel objects are shown. Only common objects were used in Experiment 3.

(B) The vertical axis is the same as for (A). Data are presented for Experiment 3 ($n = 6$) only, for the vTO, cIPS, and LOC ROIs.

(C) The vertical axis indicates the magnitude of the order effect as a difference in percent signal change between the initial presentation of object set A and initial presentation of object set B. Object set B was designated as the set of objects that was presented second. Data are presented from both Experiments 2 and 3 ($n = 8$ and $n = 6$), for the vTO and cIPS ROIs. Error bars represent sqrt[MSE/dfE].

Although many studies have shown that areas within the LOC exhibit a reduction in activity when subjects view identical images of previously presented objects (for example, see Badgaiyan, 2000; Buckner et al., 1998; James et al., 2000; Jiang et al., 2000; Squire et al., 1992; van Turennout et al., 2000; for review, see Cabeza and Nyberg, 2000; Schacter and Buckner, 1998; Wiggs and Martin, 1998), the present study shows the same bilateral reduction for rotated and identical images.

The viewpoint invariance of this repetition priming effect can be contrasted with the results of an "adaptation" study by Grill-Spector et al. (1999) and another priming study by Vuilleumier et al. (2002). Three factors could contribute to the differences between our findings and those of Grill-Spector et al. (1999). First, in their study, rotated versions of the same image were repeated during stimulus presentation blocks and compared to stimulus blocks in which the identical image was presented repeatedly at the same viewpoint. Thus, the repeated stimuli were presented immediately; unlike our study, in which repeated stimuli were presented after a delay usually of minutes. This is an important point because there is behavioral evidence that interstimulus intervals of less than 2000 ms confer view-specific benefits in object naming that are not present at longer intervals (for example, see Ellis et al. 1989). Second, the rotation that we used was shown to have a negligible effect on behavioral performance (Figure 1B), which may have not been the case with the rotations and the stimuli used in their study. Finally, as Figure 4B

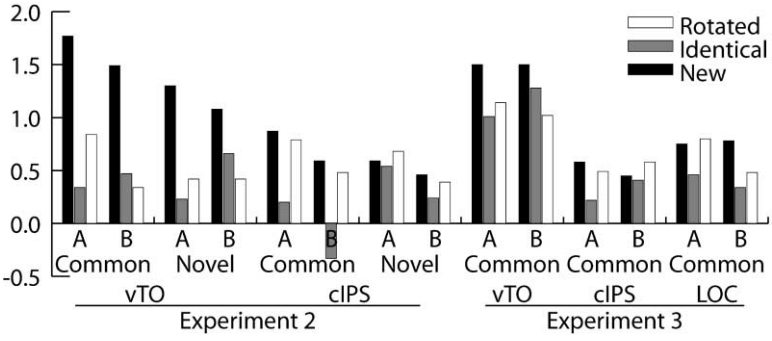

Figure 5. Activation Data from All Conditions and Regions of Interest

Data from Experiment 2 are averaged across eight subjects, and data from Experiment 3 are averaged across six subjects. Data represent right hemisphere activation, which was not significantly different from left hemisphere activation. The vertical axis represents percent signal change using scrambled object viewing as a baseline for Experiment 2 and fixation as a baseline for Experiment 3. The order of presentation of the identical and rotated conditions was counterbalanced across object sets A and B in Experiment 3. Object set A was defined as the set of objects that was presented first to the subject; however the identity of these objects was counterbalanced. New objects represent the initial presentation of an object, identical objects represent a repeated presentation at the same viewpoint, and rotated objects represent a repeated presentation at a different viewpoint.

Table 1. T-Tests for All Comparisons in Experiments 2 and 3

Contrast	Experiment 2	Experiment 3
Area vTO		
N-I	4.30[b]	2.95[a]
N-R	3.22[b]	2.38[a]
R-I	1.95[a]	0.71
Area cIPS		
N-I	4.11[b]	2.78[a]
N-R	0.62	0.48
R-I	2.20[a]	2.39[a]

N, new (initial); I, identical (repeated); R, rotated (repeated).
[a] $p < 0.05$.
[b] $p < 0.01$.

illustrates, when our vTO ROI was made larger to include all of the LOC, the pattern of activation was similar to that seen by Grill-Spector et al. (1999). Thus, we have shown that area vTO, a region within the LOC, shows more generalization across viewpoint than when the entire LOC is considered, confirming that the LOC is functionally heterogeneous.

A recent event-related study by Vuilleumier et al. (2002) also found evidence for viewpoint-independent priming in the fusiform gyrus, but only in the left hemisphere. The right fusiform gyrus showed a priming effect only with identical repetitions of objects. This lateralized effect contrasts with our finding of bilateral viewpoint-independent priming in vTO. A critical difference between their study and ours was that Vuilleumier et al. (2002) had subjects make a decision on each trial about whether they were viewing a familiar object or a nonsense object. On the surface, this small difference in methodology might not seem important. But in fact, Vuilleumier et al. (2002) found priming only with common objects; the nonsense objects produced no evidence of priming whatsoever in the fusiform gyrus or in the posterior parietal cortex. Again, this result contrasts with ours in that we found that the presentation of common objects and novel objects resulted in similar patterns of priming in both areas vTO and cIPS. In the Vuilleumier et al. (2002) study then, subjects seemed to be processing the common and nonsense objects quite differently, whereas in our study, the subjects, who were not required to make any decision about the objects, appeared to treat both sets of objects in much the same way. It is possible, therefore, that in the Vuilleumier et al. (2002) experiment right and left hemisphere processes were recruited differentially to perform the object decision task. In fact, there is additional evidence for this in their experiment: only the right posterior parietal cortex (in an area corresponding to our area cIPS) showed significant priming with identical images of objects, a result which is different from the bilateral activation that we and others have observed using a paradigm that did not involve an object decision task (Dale et al., 2000; James et al., 2000; Jiang et al., 2000).

There is actually considerable evidence that area cIPS is involved in the visual processing of objects (Dale et al., 2000; Faillenot et al., 1997; Grill-Spector et al., 2000; James et al., 2000; Kraut et al., 1997). Moreover, as was mentioned above, the object-related activation in this region is modulated by repetition priming, typically showing the same reduction in amplitude that has been observed in areas within the LOC when subjects are presented with identical images of the same object (Dale et al., 2000; James et al., 2000; Jiang et al., 2000; Vuilleumier et al., 2002). Unlike the object-related activation that we observed in area vTO, however, the activation in area cIPS in our experiment did not show a reduction in amplitude when subjects were presented with rotated images of the previously seen objects. This difference in the patterns of activation in areas vTO and cIPS suggests that different object properties may be processed in these two regions. It should be emphasized that the activation in area cIPS was sensitive to a viewpoint change that showed no effect in our behavioral task (Experiment 1). Although we cannot make a strong claim about the relationship between the fMRI data and the behavioral data, because the behavioral data were not collected at the same time that the fMRI data were, these findings suggest that activation in area vTO reflects behavioral performance and activation in area cIPS does not.

The generalization across viewpoint observed in area vTO is consistent with what one might expect to see in the ventral stream of visual processing, a network which plays a critical role in object identification and recognition. Although there is much debate about the nature of the object representations created by the ventral pathway (Biederman and Kalocsai, 1997; Tarr and Bulthoff, 1998), there is general agreement that efficient perception requires that subjects be able to recognize objects from a variety of different viewpoints. In many behavioral tasks that require judgements about objects, there is a cost associated with changes in viewpoint. Based on the results from Experiment 1, we suggest that the cost associated with the change in viewpoint that we used in Experiments 2 and 3 was negligible. Thus, it is not surprising that area vTO, which is thought to be a major component of the ventral stream, treats the same object seen from different viewpoints as identical. In other words, area vTO showed evidence of repetition priming even when the object was presented from a viewpoint that was quite different from that used in the original presentation, but was still easily identifiable.

Object processing in the dorsal pathway, which plays a critical role in the visual control of skilled actions like grasping, is likely to be quite viewpoint-dependent. The same object presented from different viewpoints will often demand quite different hand postures during grasping. Thus, one might expect that object-related activity in dorsal stream areas would not differentiate between a new object and a rotated image of an object that had been presented earlier. This is what happened in area cIPS, an area that is thought to be homologous with a region in the monkey cerebral cortex that has been implicated in the analysis of the three-dimensional structure of objects (Sakata et al., 1997). It has been proposed that this region in the monkey provides critical information about the size, orientation, and shape of goal objects for grasping movements.

The same pattern of results was found with the common and novel objects that were used in Experiment 2. For both kinds of objects, there was a reduction in object-related activation when subjects viewed objects that were identical to those they had seen earlier, al-

though the magnitude of the effect was attenuated slightly with novel objects. Moreover, the difference in the activation in areas vTO and cIPS with rotated images was essentially the same for common and novel objects. At least one other study has also found that repetition priming with novel and common objects produced similar changes in brain activation (van Turennout et al., 2000). But, the directions of the changes produced by novel object priming have not always been consistent (for discussion, see Gauthier, 2000). One reason for these discrepant results might be the level of categorization needed to differentiate the stimuli that have been used in different studies. Without exception, the studies (Henson et al., 2000; James et al., 2002; Schacter et al., 1995) that found increases in priming-related activation with novel stimuli used sets of stimuli that could be classified at the subordinate level and that were very similar in their appearance (faces or nonsense objects with similar surface or geometrical properties). There is evidence from both behavioral and neuroimaging studies that the processes underlying basic-level categorization and subordinate-level categorization are quite different (Gauthier et al., 1997; Gauthier and Tarr, 1997). What makes the novel stimuli in the present study different from others is that they varied considerably in their surface features and geometry. Indeed, they were designed to match (in size, texture, and number of parts) the set of common objects, which could be discriminated at the basic level of categorization and which were very dissimilar in their appearance.

Finally, the only difference in the pattern of results between the two fMRI experiments was the presence of a significant order effect in Experiment 2 but not Experiment 3. That is, in Experiment 2, the initial presentation of object set A produced more activation in area cIPS than did the initial presentation of object set B. These two sets of objects were presented from the same viewpoints in Experiment 2, but not in Experiment 3. The reduction in activation that occurred in Experiment 2, therefore, could be interpreted as an adaptation to object orientation independent of object identity. There was a suggestion that this "orientation priming" effect was larger in area cIPS—the area we have implicated in the visual control of object-directed action. More investigation of the orientation priming effect is needed, however, before any strong claims can be made about its function or its localization to specific brain regions. Regardless, the fact that the order effects were very small in Experiment 3 precludes the speculation that our results could have been due simply to order effects rather than priming effects.

An alternative conclusion based on our data is that regions that show high object selectivity also show generalization across viewpoint. Area vTO in both Experiments 2 and 3 was the most highly object-selective region of cortex, as defined by the comparison of intact object viewing and scrambled object viewing. Area vTO was also showed the highest degree of generalization across viewpoint. Also, we cannot claim absolutely that area cIPS is sensitive to viewpoint. It is likely that changing the viewpoint of the object changes many low-level characteristics. It is possible that the activation in area cIPS might be sensitive to one of these low-level characteristics, but not all of them.

Nevertheless, the results of the present study reveal a clear difference between the effects of priming on activation in areas vTO and cIPS. Priming in area vTO showed generalization across viewpoints, responding similarly to identical and rotated images of the objects presented earlier. In sharp contrast, area cIPS showed priming only with identical images, and appeared to treat the rotated images as new objects. It should be pointed out, however, that these experiments explored the effects of only one angle of rotation in depth. Other rotations might have produced a different pattern of results. For example, very large rotations, or the use of "unusual views" of the objects, might have produced less priming in area vTO. By the same token, very small rotations might have allowed for priming in area cIPS. Despite having data for only the 60° rotation, our results suggest that there is a fundamental difference in the "tuning" functions of these two regions for object viewpoint. Clearly, more work is needed to fully characterize these tuning functions, but the results of our study suggest that the function is more broadly tuned in area vTO than in area cIPS. This difference in the tuning functions probably reflects the respective roles of the two areas in visual processing. Area vTO is part of the ventral stream of visual processing, a network dedicated to the perception and recognition of objects. Therefore, this area would be expected to show broad generalization across viewpoints. Area cIPS is part of the dorsal stream of visual processing, a network mediating the visual-motor transformations required for object-directed action. This area would be expected to be quite sensitive to changes in object viewpoint, and perhaps especially sensitive when the viewpoint change necessitates a change in the grasping action that is directed at the object.

Experimental Procedures

Subjects

Nineteen subjects participated in Experiment 1, eight subjects participated in Experiment 2, and six subjects participated in Experiment 3. All subjects were right-handed, reported normal or corrected-to-normal visual acuity, and had no known neurological or visual disorders. Ages ranged from 25 to 34 years with a mean age of 29.3 years. The ethical review boards of both the University of Western Ontario and the Robarts Research Institute approved a protocol for the procedure.

Stimuli and Apparatus

All stimuli were images of objects rendered with three-dimensional modeling software. A set of 24 common objects was selected from the TarrLab Object Databank (see http://www.cog.brown.edu/tarr). The 24 objects were chosen such that no two objects would be classified at the same basic level of categorization. Also, only objects with a definable principal axis of elongation were chosen. Images of the objects were selected from the databank at four different orientations, 30°, 330°, 150°, and 210° (Figure 1A). Only the 30° and 330° views were used in Experiments 1 and 2, but all four views were used in Experiment 3. In Experiments 1 and 2, a set of novel objects were designed to match the common objects on certain characteristics, including having a principal axis of elongation, having a definable bottom, and having the same number of object parts and surface textures. Images were converted to gray scale, and the intensities of each image were scaled such that the mean intensity of every image was identical. For the control conditions in Experiments 2 and 3, scrambled versions of the images of the objects were used. Images were scrambled by dividing each image

into 2304 squares in a 48 × 48 grid pattern. These squares were then randomly exchanged within each image. A similarity index (correlation of image intensity) was calculated on a subset of the objects. Between the 30° and 330° views, the average correlation was 0.11; between the 150° and 210° views, the average correlation was 0.15; and between the 30° view and the scrambled image, the average correlation was 0.00.

For Experiment 1, images were presented on a computer monitor 57 cm in front of the subject and the objects subtended between 1.5° and 2.7° of visual angle. For Experiments 2 and 3, images were rear projected onto a screen that straddled the subject's waist while they lay supine in the fMRI scanner. Subjects were able to view the back projection screen through a mirror that was suspended from the top of the head coil. Total viewing distance was 75 cm and the objects subtended between 2.0° and 3.5° of visual angle depending on the length and orientation of the object's principal axis of elongation.

Stimulus Presentation

In Experiment 1, subjects performed a sequential matching task. Events occurred in the following order: fixation cross (750 ms), sample stimulus (1200 ms), mask (250 ms), and match stimulus (until response). Subjects were instructed to press one of two buttons indicating whether the pair of objects was the same or different, regardless of their orientation.

In Experiments 2 and 3, subjects passively viewed intact and scrambled images of the objects in a blocked imaging paradigm. During all runs, both intact and scrambled images of the objects were presented. For Experiment 2, data were collected in two runs (Figure 1A). Each run began with a 27 s presentation of a fixation cross during which subjects were instructed to fixate. After the fixation period, intact and scrambled images of the objects were presented in eight alternating 27 s periods. Identical sets of intact objects were presented in the first and second runs. For both runs, the first intact image period consisted of 12 of the 24 objects (set A) being presented at the 30° view, the second period consisted of the remaining 12 objects (set B) being presented at the 30° view, the third period consisted of the objects in set A being presented at the 330° view, and the fourth period consisted of the objects in set B being presented at the 330° view. Each image, whether intact or scrambled, was presented for 2.25 s.

In Experiment 3, data were collect in a single run (Figure 1A). Each run began and ended with an 18 s fixation period. After the first fixation period, intact and scrambled images of the objects were presented in 12 alternating 18 s periods. The first intact image period consisted of 12 of the 24 objects (set A) being presented at the 30° view, the second period consisted of a repeated presentation of object set A, at the identical 30° view, and the third period consisted of the presentation of object set A at a rotated 330° view. Intact image periods four through six were the same as periods one through three except that object set B was used and the order of presentation of the identical and rotated repetitions were counterbalanced.

Imaging Parameters and Analysis

All imaging was done using a 4 Tesla, whole-body MRI system (Varian/Siemens) and a quadrature head coil located at the Robarts Research Institute (London, ON, Canada). The field of view was 19.2 × 19.2 × 7.5 cm, with an in-plane resolution of 64 × 64 pixels and 15 contiguous coronal scan planes per volume, resulting in a voxel size of 3.0 × 3.0 × 5.0 mm. These 15 scan planes extended from the occipital pole to approximately the center of the corpus callosum. Images were collected using a T2*-weighted, segmented (navigator corrected), interleaved EPI acquisition (TE = 15 ms, TR = 500 ms, flip angle = 30°, two segments/plane) for blood oxygen-level-dependent (BOLD)-based imaging (Ogawa et al., 1993). Each volume (15 scan planes) required 1.5 s to acquire. High-resolution T1-weighted anatomical volumes were also acquired using a 3D magnetization-prepared (MP) turbo FLASH acquisition (TI = 600 ms, TE = 5.2 ms, TR=10 ms, FA=15°).

The imaging data were preprocessed using the Brain Voyager 3D analysis tools. The anatomical volumes were transformed into a brain space that was common for all subjects (Talairach and Tournoux, 1988). Functional volumes for each subject underwent 3D motion correction, 3D spatial frequency filtering with a frequency window between 2 and 24 cycles, and temporal frequency filtering with a frequency window between 2 and 60 cycles. These preprocessed functional volumes were aligned to the transformed anatomical volumes, thereby transforming the functional data into a common brain space across subjects.

The imaging data were analyzed using the Brain Voyager multi-study GLM (general linear model) procedure. This procedure allows the correlation of predictor variables or functions with the recorded activation data (criterion variables) across scanning sessions. A fixed-effects model was used. The predictor functions that were used were a series of γ functions ($\Delta = 2.5$, $\tau = 1.25$) spaced in time based on the blocked stimulus presentation paradigm for the particular run being analyzed (Figure 1). The data from the two separate runs in Experiment 1 were standardized using the initial fixation period as a reference. Percent signal change scores were calculated using the scrambled object blocks as the baseline for Experiment 2 and using the fixation blocks as the baseline for Experiment 3. Hemodynamic shifts were calculated separately for each subject, with 13 subjects requiring a shift of three images (6 s) and 1 subject requiring a shift of two images (4 s).

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