

A double dissociation between sensitivity to changes in object identity and object orientation in the ventral and dorsal visual streams: A human fMRI study

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Abstract

We used an event-related fMR-adaptation paradigm to investigate changes in BOLD activity in the dorsal and ventral visual streams as a function of object identity and object orientation. Participants viewed successive paired images of real-world, graspable objects, separated by a visual mask. The second image of each pair was either: (i) the same as the first image, (ii) different only in identity, (iii) different only in orientation, or (iv) different in both identity and orientation. A region in the parieto-occipital cortex (dorsal stream) showed a selective increase in BOLD activity with changes in object orientation, but was insensitive to changes in object identity. In contrast, a region in the temporo-occipital cortex (ventral stream) showed a selective increase in activity with changes in identity, but was insensitive to changes in orientation. The differential sensitivity to orientation and identity is consistent with the idea that the dorsal stream plays a critical role in the visual control of object-directed actions while the ventral stream plays a critical role in object perception.

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1. Introduction

Over 10 years ago, Goodale and Milner (Goodale & Milner, 1992) proposed that the visual mechanisms mediating our perception of objects are quite separate from those mediating the immediate control of actions directed at those objects. According to Goodale and Milner, it is this duplex nature of vision that drove the emergence of distinct visual pathways in the primate cerebral cortex. The ventral ‘perceptual’ stream, which projects from early visual areas to the temporal lobe, provides the rich and detailed representation of the world required for cognitive operations such as recognition and identification. In contrast, the dorsal ‘action’ stream,

which projects from early visual areas to the posterior parietal cortex, provides flexible control of more primitive subcortical visuomotor modules for the control of motor acts. Note that this is *not* the distinction between ‘what’ and ‘where’ (object vision and spatial vision) that was originally put forward by Ungerleider and Mishkin (1982). In Goodale and Milner’s re-interpretation, the structural and spatial attributes of a goal object are processed by both streams, but for different purposes. In the case of the ventral stream, information about a broad range of object parameters is transformed for perceptual purposes; in the case of the dorsal stream, some of these same object parameters are transformed for the control of actions. This is not to say that the distribution of visual inputs does not differ between the two streams, but rather that the main difference lies in the nature of the transformations that each stream performs on those two sets of inputs.

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Although much of the early evidence for the division of labor between the ventral and dorsal streams came from work with neurological patients (Goodale, Milner, Jakobson, & Carey, 1991; Jakobson, Archibald, Carey, & Goodale, 1991; Perenin & Vighetto, 1988) and neurophysiological studies in monkeys (for review, see Andersen & Buneo, 2003; Sakata, 2003; Tanaka, 2003), a great deal of additional support has come from functional magnetic resonance imaging (fMRI) studies in humans. In the ventral stream, areas within the lateral occipital complex (LOC), a region in the occipito-temporal cortex, are selectively activated by images of objects (for review, see Grill-Spector, 2003; Malach, Levy, & Hasson, 2002). Although there is considerable debate about the specialization of different areas within the LOC, it is generally agreed that this region plays a critical role in object recognition.

In the dorsal stream, the picture is quite different. Discrete areas in and around the intraparietal sulcus (IPS) in the posterior parietal cortex have been shown to be involved in transforming visual information into eye movements, reaching movements, grasping, and other skilled actions (for review, see Culham & Kanwisher, 2001; Goodale & Westwood, 2004). But in addition, some studies have also found that regions around the caudal part of the IPS (cIPS) and/or the adjacent occipito-parietal junction (OPJ) are activated by the simple presentation of objects, without any accompanying action (Dale et al., 2000; Faillenot, Toni, Decety, Gregoire, & Jeannerod, 1997; Grill-Spector et al., 1999; James, Humphrey, Gati, Menon, & Goodale, 2000, 2002; Kraut, Hart, Soher, & Gordon, 1997; Vuilleumier, Henson, Driver, & Dolan, 2002). It has been suggested that the activity in these early dorsal-stream areas may reflect object processing for actions, such as grasping. According to this account, these areas then send information to more anterior regions in the IPS (such as area AIP) that together with associated premotor areas perform the requisite transformations for specific effectors such as the hand (James et al., 2002; Sakata, Taira, Kusunoki, Murata, & Tanaka, 1997).

Some support for the idea that areas in the occipito-temporal cortex play a role in object recognition whereas areas in the occipito-parietal region play a role in object-directed action also comes from imaging studies that have used adaptation paradigms (James et al., 2002; Vuilleumier et al., 2002). James et al., for example, found that a region within the LOC near the ventral temporo-occipital junction (area vTO) showed adaptation for both identical and depth-rotated images of common objects. In other words, activation in this region decreased with subsequent presentations of the same object irrespective of whether the object was presented from the same or a different viewpoint. Vuilleumier et al. also showed a similar viewpoint-independent effect but only in the ventral stream of the left hemisphere.

Both James et al. (2002) and Vuilleumier et al. (2002) found that a region in the caudal part of the intraparietal sulcus that was activated by the presentation of objects showed evidence of adaptation only with identical presentations of

the same object. Rotated views of the object were treated as new objects. However, what is not clear from either of these studies is whether or not this dorsal stream sensitivity is specific to object orientation. That is, perhaps the response sensitivity within this parieto-occipital region is selective for changes in object orientation and not identity. Alternatively, the region could show sensitivity to both types of change, rebounding from adaptation in response to changes in either the identity or the orientation of the object. The block design used by James et al. (2002) did not allow them to distinguish between these two possibilities. Yet, as discussed earlier, the two visual systems account of Goodale and Milner (1992) would predict that the ventral stream, which plays a critical role in experiential perception of objects, would be particularly sensitive to changes in identity, whereas the dorsal stream, which plays a critical role in the control of object-directed actions, would be particularly sensitive to changes in object orientation (with respect to the observer).

In the present experiment we tested these predictions using an event-related fMRI design in which we presented subjects with images of two common objects, one after the other, separated by a brief mask. The identity and the orientation of the two objects could be independently changed between presentations. There were four possibilities: neither the identity nor the orientation changed (No Δ); only identity changed (Ident Δ); only orientation changed (Orient Δ); or both changed (Both Δ). To localize regions that were sensitive to changes in identity and those that were sensitive to changes in orientation, we carried out two independent contrasts. In the first, we compared the pattern of activation associated with Ident Δ to that associated with No Δ . In the second, we compared the pattern of activation associated with Orient Δ to that associated with No Δ . We found an identity-sensitive region in area vTO in the ventral stream and an orientation-sensitive region at the occipito-parietal junction (OPJ) in the dorsal stream. When we examined the activity in these regions across all four events, we found that area vTO was selectively sensitive to changes in identity and was not influenced by changes in orientation [(Both Δ = Ident Δ) > (Orient Δ = No Δ)] whereas area OPJ was sensitive to changes in orientation and was not influenced by changes in identity [(Both Δ = Orient Δ) > (Ident Δ = No Δ)]. These results lend additional support to the idea that the ventral stream plays a critical role in object perception whereas the dorsal stream is more involved in the visual control of actions that might be directed at those objects.

2. Method

2.1. Subjects

Seven neurologically healthy individuals (four female, three male) participated in the study. All were right handed, with normal or corrected-to-normal visual acuity. Each participant provided informed consent according to procedures

approved by the University of Western Ontario Review Board for Health Sciences Research Involving Human Subjects.

2.2. Stimuli

Visual stimuli were presented using a PC laptop connected to a video projector. Images were projected onto a rear-projection screen which straddled the subject's waist while they lay supine in the scanner. Subjects viewed the screen via a mirror mounted to the head coil. Stimulus programs were created using a custom application with Microsoft Visual C++ (version 6). Two-dimensional greyscale photographs of real-world graspable objects were selected as stimuli using the Hemera Photo-Objects image database (version 2.0). A total of 120 different images were used. Only objects with a clear principal axis of elongation were used. The mask stimulus was generated using Matlab to divide the image into a 25×25 grid and then randomly reorder the cells of the grid.

2.3. Procedure

Each event-related experimental scan was 332 s in length. Participants were instructed to maintain fixation throughout the entire scan and to view the stimuli passively. Each scan comprised 16 stimulus events, each separated by blank fixation periods (ranging from 12 to 15 s), which were

long enough to allow the blood oxygenation-level-dependent (BOLD) signal to return to baseline levels. Fig. 1 illustrates the four different types of events (No Δ , Ident Δ , Orient Δ , and Both Δ) that were presented in each scan. Each event type comprised the following: a prime stimulus (1.25 s), followed by a mask (1.25 s), followed by a target stimulus (1.25 s), ending with a mask (1.25 s). The target stimulus was either exactly the same as the prime (No Δ), different from the prime only in identity (Ident Δ), different from the prime only in orientation (Orient Δ), or different from the prime in both identity and orientation (Both Δ). This led to a total of four event types plus the rest condition. Each of the event types occurred four times during a single scan. In all events, object orientations were limited to two possibilities: each object's principal axis was tilted 45° in-plane clockwise or counter-clockwise from the horizontal meridian. A total of 24 different object identities were used during a single scan. Objects were randomly assigned to an event type and were not repeated across scans. Event types were randomly distributed within and across scans.

Each session also included a single 'localizer' scan, 124 s in length, designed to engage the critical regions involved in the execution of saccadic eye movements. The scan was divided into alternating epochs of fixation and saccades. During fixation epochs, participants were instructed to maintain fixation on a cross-situated centrally in the display. During

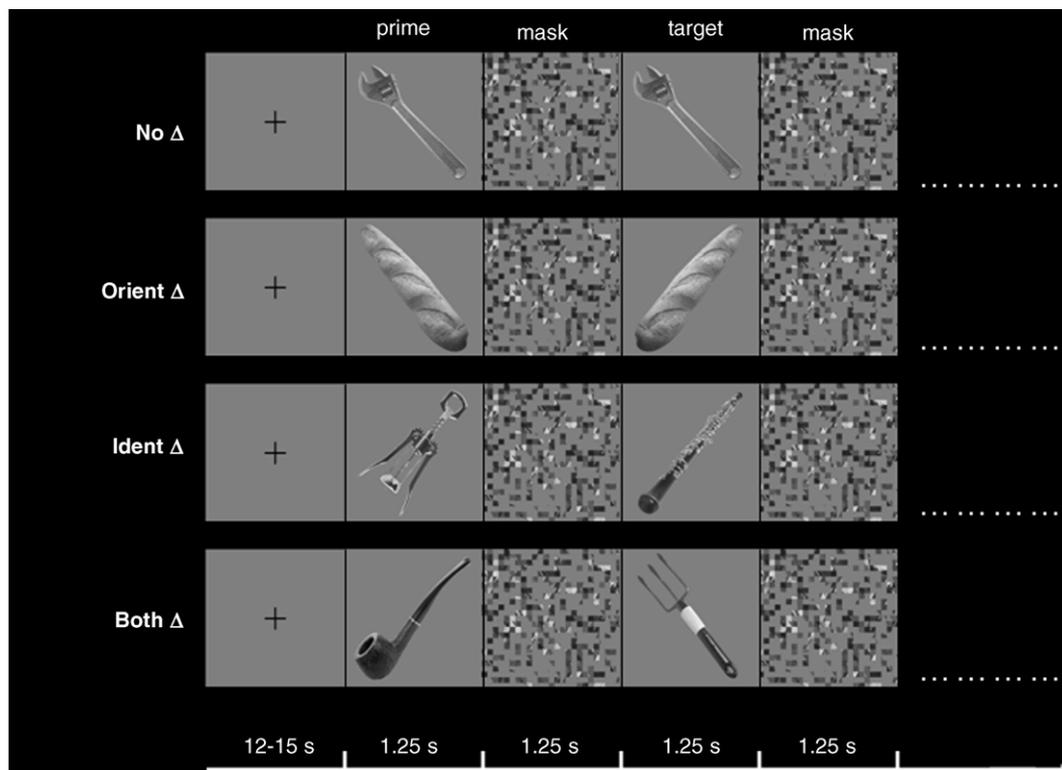


Fig. 1. Experimental stimuli, timing, and event types. All experimental stimuli were two-dimensional real-world graspable objects, tilted 45° in-plane to the right or 45° in-plane to the left of the horizontal meridian with respect to the observer. Each event comprised a prime stimulus, followed by a mask, a target stimulus, and finally a mask. Possible examples of the four different event types are shown. The stimulus timeline is shown at the bottom of the figure.

saccade epochs, participants were instructed to perform lateral saccadic eye movements between two locations at the sides of the display. Each epoch was 30 s in length. The purpose of this scan was two-fold. First, it enabled us to identify the lateral intraparietal area (LIP), which could then be used as a reference point in the dorsal stream to localize the relative position of areas that we identified in the main experiment. Second, by assessing the pattern of activity within area LIP during our experimental scans, we could evaluate whether or not confounding factors such as eye movements and/or shifts in spatial attention differed across the conditions of interest.

2.4. Imaging parameters

All imaging was done using a 4 T, whole-body MRI system (Varian/Siemens) and a quadrature radiofrequency head coil, located at the Robarts Research Institute (London, ON, Canada). Each imaging session consisted of six functional scans and a high-resolution anatomical scan. Functional volumes were collected using a T2*-weighted, segmented (navigator corrected), interleaved EPI acquisition (TE = 150 ms, TR = 500 ms, FA = 45°, two segments/plane) for BOLD-based imaging (Ogawa et al., 1992). The field of view was 19.2 cm × 19.2 cm, with an in-plane resolution of 64 × 64 pixels and 11 contiguous pseudo-coronal scan plans per volume, resulting in a voxel size of 3.0 mm × 3.0 mm × 5.0 mm. These 11 scan plans extended from the occipital pole to approximately the posterior edge of the corpus callosum. Each volume required 1 s to acquire. High-resolution T1-weighted anatomical volumes were acquired using 3D magnetization-prepared FLASH acquisition (TI = 500 ms, TE = 6 ms, TR = 12 ms, FA = 11°).

2.5. Data processing and analysis

The imaging data were preprocessed and analyzed using Brain Voyager 2000 (Brain Innovation, Maastricht, The Netherlands). Anatomical volumes were transformed into standard stereotaxic space (Talairach & Tournoux, 1988). Two functional scans from two separate subjects were excluded from the analysis due to image acquisition difficulties. The Brain Voyager 3D motion correction parameter plots were used to screen each functional scan for subject head motion. One scan was found to be significantly contaminated with head motion and was thus removed from further analysis. Functional volumes for each subject underwent high-pass temporal frequency filtering (frequency window of between 0 and 2 cycles per scan) in order to remove any low frequency trends in the signal. Functional volumes were then aligned to the transformed anatomical volumes, thereby transforming the functional data into a common brain space across subjects.

The imaging data were analyzed using a general linear model (GLM) to evaluate the contribution of each of

the four event types to the overall variability of the data. This procedure allows the correlation of predictor functions with the activation data within each voxel in and across scanning sessions. Predictors were γ functions ($\Delta = 2.5$, $\tau = 1.25$), designed to estimate hemodynamic response properties (Boynton, Engel, Glover, & Heeger, 1996), spaced in time to coincide with stimulus events. A predictor of no interest, corresponding to the presentation of the first stimulus in each event, was also included in the model. Functional data from all subjects were first z-normalized before analyzing them with the Brain Voyager multi-study analysis tool. A correction for serial correlations was applied to the data. Two independent contrasts were then performed in order to identify regions of interest. To identify regions showing sensitivity to changes in object orientation activation associated with the Orient Δ condition was contrasted against activation associated with the No Δ condition. To identify regions showing sensitivity to changes in object identity activation associated with the Ident Δ condition was contrasted against activation associated with the No Δ condition. Statistical activation maps were set to reliable threshold levels and cluster volumes ($p < .02$, minimum cluster size = 189 mm³) using Monte Carlo simulations (performed with AlphaSim software, courtesy of Douglas Ward, Medical College of Wisconsin) to verify that our regions of interest were unlikely to have arisen due to chance (corrected $p < .05$), given the problem of multiple comparisons.

To confirm that the regions we identified were truly sensitive to the dimensions in question, we also performed post hoc contrasts between the two other pairs of events that differed in the critical dimension but had not been used to define the region. On the basis of subtraction logic, the two ‘orientation’ contrasts, namely Orient Δ versus No Δ and Both Δ versus Ident Δ , would reveal activity associated with a change in orientation. Similarly, the two ‘identity’ contrasts, namely Ident Δ versus No Δ and Both Δ versus Orient Δ , would reveal activity associated with a change in identity. Thus, in areas identified by the contrast between Orient Δ versus No Δ , we performed a post hoc contrast between Both Δ versus Ident Δ . Similarly, in areas identified by the contrast between Ident Δ versus No Δ , we performed a post hoc contrast between Both Δ versus Orient Δ .

To determine how selective the activation in each area was to the dimension in question, we carried out two additional post hoc contrasts. Thus, we evaluated whether orientation-sensitive regions would show significant activation to the two contrasts that included a change in identity (Ident Δ versus No Δ and Both Δ versus Orient Δ) and whether identity-sensitive regions would show significant activation to the two contrasts that included a change in orientation (Orient Δ versus No Δ ; and Both Δ versus Ident Δ).

In order to be confident that the effects identified in the combined group analyses were consistent across individuals, additional analyses were performed on an individual subject basis. For each individual, the same two independent comparisons used to identify regions of interest within the

combined group data were performed. As in the group analysis, regions responsive to changes in object orientation, were selected by subtracting the activity associated with the No Δ event from that associated with the Orient Δ event. Similarly, regions responsive to changes in object identity, were selected by subtracting the activity associated with the No Δ event from that associated with the Ident Δ event. fMRI adaptation experiments do not typically evaluate data on an individual basis because the effects can be weaker than with other fMRI experiments. Nevertheless, in our data we found that at relatively liberal thresholds ($p < .05$, uncorrected), activation could be observed in the data from six of seven subjects within each of the two main areas identified in the group analysis. Obviously, these thresholds were very liberal; however, we once again evaluated the activity of each area using the additional (and independent) post hoc contrasts that had not been used to define those areas. If the thresholds had been unacceptably low such that the difference in the defining contrast was due to chance, it would be highly unlikely to find any replication in separate and independent contrasts that differed in the same key dimension. The post hoc contrasts were paired t -tests performed on the beta weights associated with each of the four event-types extracted from the identified regions in individual subject's data. Once again, as in the group analysis, the contrasts of particular interest were those that evaluated the contributions of the two key factors – orientation change and identity change – in contrasts other than those used to define the region.

Data from the saccade ‘localizer’ scans were also analyzed using a GLM. Thus, a predictor function, convolved with the hemodynamic response, time-locked to saccade epochs, was used to build the design matrix. Area LIP was identified bilaterally in each subject by contrasting the activation associated with the saccade condition against the activation associated with the fixation baseline. Statistical thresholds were increased until an independent focus of activation was identified along the intraparietal sulcus of each hemisphere. Talairach coordinates describing the location of area LIP in previous imaging studies of saccadic eye movements (Konen, Kleiser, Wittsack, Bremmer, & Seitz, 2004; Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002) were used to ensure that the focus of activation localized in each subject corresponded to area LIP. For each individual, the pattern of activation within area LIP during experimental scans, averaged across both hemispheres, was assessed by comparing the beta weights for each of the four stimulus events.

3. Results

3.1. Combined subject analysis

By measuring the averaged BOLD response to the Orient Δ condition against a baseline activation associated with the No Δ condition, we found an area showing sensitivity

to a ‘pure’ change in object orientation in the dorsal-stream regions of the right hemisphere. The cluster of activation corresponded to area OPJ (Fig. 2A). The averaged time course of activation within this cluster is plotted for each of the four experimental conditions (Fig. 2A). Post hoc comparisons demonstrated not only *sensitivity* to orientation changes, but *selectivity* for orientation; that is, the BOLD response within the region showed definite sensitivity to changes in object orientation (Both $\Delta > \text{Ident } \Delta$, $p < .01$) but was not sensitive to changes in object identity (Ident $\Delta = \text{No } \Delta$, $p = .12$; Both $\Delta = \text{Orient } \Delta$, $p = .67$).

The corresponding comparison for identity (Ident Δ against No Δ) revealed a distinct cluster of activation within the ventral stream in the right hemisphere that was sensitive to changes in object identity. The location and averaged time course data for this region are presented in Fig. 2B. The region, which appeared to be in the same location as area vTO identified by James et al. (2002), demonstrated sensitivity for changes in identity (Both $\Delta > \text{Orient } \Delta$, $p < .05$), showing no sensitivity to changes in object orientation across the two object presentations (Orient $\Delta = \text{No } \Delta$, $p = .83$; Both $\Delta = \text{Ident } \Delta$, $p = .2$).

3.2. Individual subject analysis

The same two comparisons described in the combined subject analysis were performed on the data from each individual subject in order to assess the distribution and consistency of the effects across individuals. Resultant activation maps were evaluated for functional-anatomical consistency across individuals. For each contrast map, an area of interest, referred to as either OPJ (for the Orient Δ versus No Δ contrast) or vTO (for the Ident Δ versus No Δ contrast), was identified based on the anatomy of the individual. Area OPJ encompasses part of the superior occipital gyrus and much of the posterior intraparietal sulcus including the junction point of the intraparietal and the transverse occipital sulci. Area vTO encompasses parts of the temporo-occipital incisure and the lateral occipital temporal sulcus and includes posterior portions of both the inferior temporal and fusiform gyri (Duvernoy & Bourgoin, 1999). Both areas are lateralized to the right hemisphere. These anatomical landmarks were used to help characterize clusters of activity within each individual as region OPJ and vTO, respectively. All other active clusters were collected and compared across individuals for spatial-anatomical consistency.

Fig. 3A shows the results of this procedure for the Orient Δ versus No Δ comparison. The only area reliably identified across individuals was that corresponding to OPJ. The region was identified in six out of the seven individuals tested. The bar graph in the Fig. 3A shows the computed beta weights extracted from the region for each individual for each event type. The mean beta weights associated with the four event types, averaged across individuals, are also shown. Post hoc comparisons revealed the same pattern of response specificity within this region as that described in area OPJ based on the

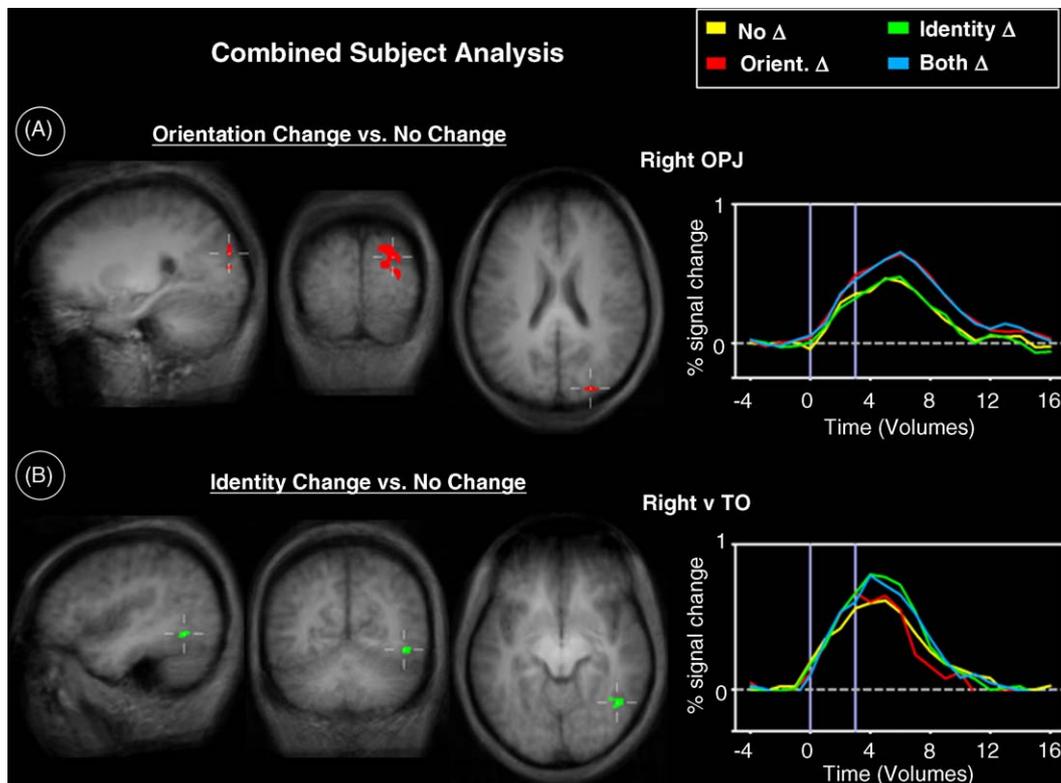


Fig. 2. Results of the combined subject analysis. Activation maps were computed from Talairach averaged group data and are shown on the combined subjects' anatomical image. (A) Area OPJ (Talairach coordinates: $x=22$, $y=-81$, $z=19$) was identified by contrasting activation associated with the Orient Δ event with that associated with the No Δ event. To the right of the contrast map, the averaged event-related time course is plotted. A specific sensitivity to changes in object orientation but not identity is evident in the pattern of averaged responses. (B) Area vTO (Talairach coordinates: $x=42$, $y=-55$, $z=-6$) was identified by contrasting activation associated with the Ident Δ event with that associated with the No Δ event. To the right of the contrast map, the averaged event-related time course is plotted. A specific sensitivity to changes in object identity but not orientation is evident in the pattern of averaged responses.

combined subject analysis. Explicitly, the region was preferentially responsive to changes in object orientation (Both $\Delta > \text{Ident } \Delta$, $p < .005$) but was not responsive to changes in object identity (Ident $\Delta = \text{No } \Delta$, $p = .11$; Both $\Delta = \text{Orient } \Delta$, $p = .06$). Thus, employing an analysis procedure that is sensitive to potential response variations across individuals demonstrated a pattern of activity within area OPJ that was specific to changes in object orientation.

Fig. 3B shows the results of this procedure for the Ident Δ versus No Δ contrast. The only area reliably identified across individuals was that corresponding to vTO. The region was identified in six out of the seven individuals tested. The bar graph in Fig. 3B shows the computed beta weights extracted from the region for each individual for each event type. The mean beta weights associated with the four event types, averaged across individuals, are also shown. Post hoc comparisons revealed a pattern of response selectivity specific to changes in object identity. Specifically, the region was sensitive to changes in object identity (Both $\Delta > \text{Orient } \Delta$, $p < .05$) but was not responsive to changes in object orientation (Orient $\Delta = \text{No } \Delta$, $p = .79$; Both $\Delta = \text{Ident } \Delta$, $p = .18$). These results replicate the findings for area vTO described in the combined group analysis.

3.3. LIP localizer: ROI-based analysis

In order to eliminate the possibility that the above effects could partially be explained by differences in the number of eye movements across the conditions, a region of interest (ROI) analysis was performed. Previous imaging studies have identified the lateral intraparietal area (LIP) as a critical neural substrate involved in the execution of rapid eye movements (e.g., Muri, Iba-Zizen, Derosier, Cabanis, & Pierrot-Deseilligny, 1996). Thus, if our experimental conditions are confounded by unequal amounts of eye movements, then the pattern of activity within LIP should reflect these differences. LIP was localized bilaterally in each subject by contrasting the activation associated with the saccade condition against the activation associated with the fixation baseline. Fig. 4 shows the results of this procedure superimposed on the anatomy of a single individual. In the bottom half of Fig. 4, the computed beta weights associated with each of the four event types for each individual are plotted. Post hoc comparisons of the mean beta weights, averaged across subjects, revealed no significant differences between any of the conditions. Therefore, the effects described in area OPJ and vTO are unlikely to be related to

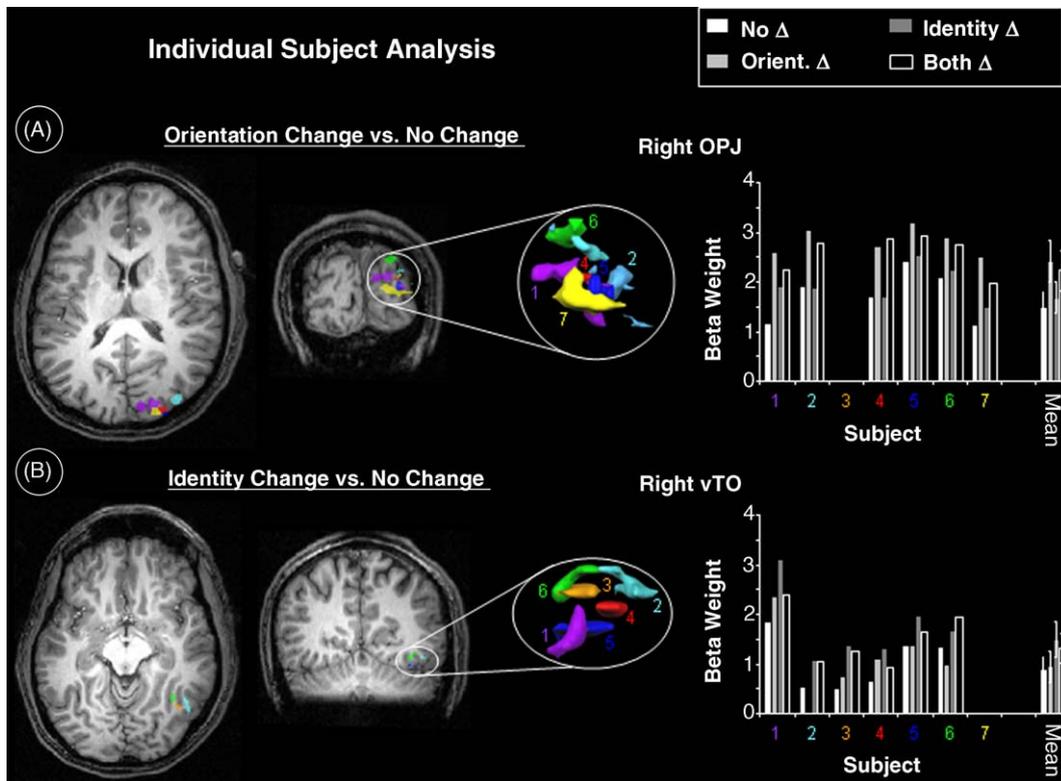


Fig. 3. Results of the individual subject analysis. Regions of activity were identified in each individual and are shown superimposed on the anatomy of a single subject (which is not representative of the sulcal patterns for all subjects). (A) Area OPJ was identified by contrasting activation associated with the Orient Δ event with that associated with the No Δ event. To the right of the contrast map, the beta weights extracted from the region identified in each individual are plotted. Comparisons of the mean beta weights demonstrate a pattern of response sensitivity selective for changes in object orientation and not identity. (B) Area vTO was identified by contrasting activation associated with the Ident Δ event with that associated with the No Δ event. To the right of the contrast map, the beta weights extracted from the region identified in each individual are plotted. Comparisons of the mean beta weights demonstrate a pattern of response sensitivity selective for changes in object identity and not orientation.

differential amounts of saccadic eye movements across event types.

4. Discussion

The results of the present experiment reveal a striking difference in the sensitivity of dorsal and ventral stream visual areas to changes in object orientation and object identity. A discrete region in and around the posterior portions of the intraparietal sulcus, area OPJ, showed a robust increase in BOLD activity in response to a change in the orientation of an object but no change in activity in response to a change in object identity. The opposite pattern of activity was seen in a discrete region posterior to the fusiform gyrus, (area vTO). This region showed selective increases in BOLD activity in response to changes in object identity but not orientation. Although the identity-specific activation in area vTO is not surprising given the findings of earlier fMRI studies that used similar experimental designs (e.g., James et al., 2002; Vuilleumier et al., 2002), the orientation-specific activation we observed in area OPJ is a novel finding; the pattern of activation in OPJ does not generalize to changes in object identity (i.e. it shows ‘identity-invariance’).

What is the underlying nature of this orientation selectivity? First, we must consider the possibility that the orientation effects are not at all related to higher-level object processing. For instance, perhaps the effects are entirely due to shifts in spatial attention. That is, in those events involving a change in the orientation of the target object, relative to the initial prime, perhaps the parietal-occipital activation we observed was in fact driven by a differential amount of spatial attention allotted to such events compared to those in which orientation changes did not occur. However, previous imaging studies describe the lateral intraparietal area (LIP), along with other parietal regions, as being highly responsive to both saccadic eye movements and shifts in spatial attention (Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001; Berman et al., 1999; for review, see Corbetta, 1998; Corbetta et al., 1998). Thus, if the effects we described in area OPJ are related to shifts in spatial attention, then why were these regions, previously shown to be highly responsive to such attentional shifts, not detected as well? Indeed the regions described by others as sensitive to spatial-attentional demands (including LIP) seem to be situated much more dorsal and anterior to the orientation effects we localize here. Moreover, we were able to localize area LIP in each individual and independently assess the activation within the region during our experi-

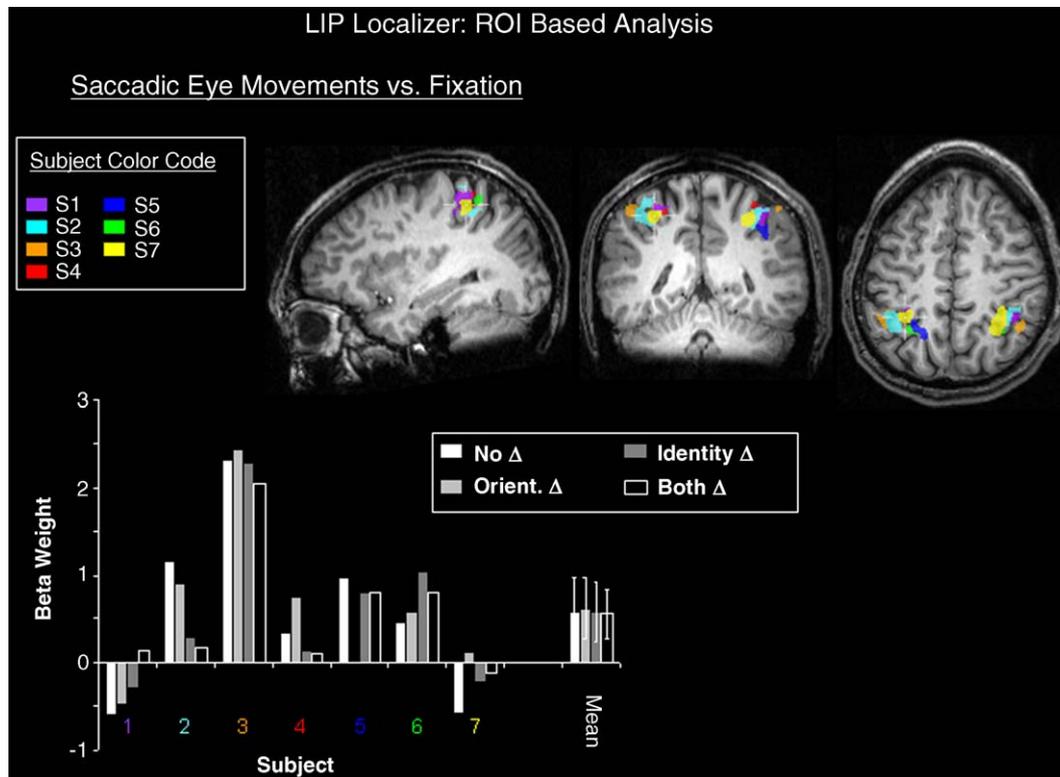


Fig. 4. Results from the LIP localizer. Regions of interest were identified bilaterally in each individual and are shown superimposed on the anatomy of a single subject (which is not representative of the sulcal patterns for all subjects). Regions were defined as area LIP by contrasting activation associated with saccadic eye movements with that associated with fixation baseline. Beta weights extracted from the region identified in each individual are plotted below. Comparisons of the mean beta weights revealed no significant differences across event types.

mental manipulations. Given that the pattern of activation within LIP was not found to differ across the four event types (Fig. 4), the possibility that the orientation effects found in area OPJ were in fact related to spatial attention seems very unlikely.

The same logic can be applied to rule out the possibility that the orientation effects we find in the occipital-parietal cortex may be linked to disparate levels of motion-related processing across our event types. If this were indeed the case, we would expect the well known motion complex (V5/MT+) to be preferentially engaged by those events involving an orientation change. No such differential activation was observed. The location of area MT+ has been well described (e.g. Dumoulin et al., 2000; Tootell et al., 1995) making it particularly easy to identify on the anatomical scan. Thus, by using salient anatomical landmarks and probing the activation in this region, we were able to rule out the presence of differential amounts of MT+ activation across the four conditions. Furthermore, we believe the mask stimulus would serve to minimize such transient motion effects that may have otherwise been unequal across events.

A final possibility to consider is that the orientation effects may have simply reflected differences in the pattern of retinotopic activation, which could have been greater for changes in orientation than for changes in identity. This is unlikely, however, since activation of highly retinotopic regions, such

as the early visual areas of the striate cortex, did not differ between the two conditions. In a related argument, it may have been the case that the orientation effects observed in the OPJ reflected not adaptation to the object itself but rather adaptation to the orientation of the low-level features that constituted that object—adaptation that would initially occur in early retinotopic areas that code for orientation. Indeed, Boynton and Finney (2003) have reported orientation-specific adaptation effects in early visual cortex using simple gratings as stimuli. But we did not observe such effects with the stimuli we used. Moreover, the presence of the mask stimulus would effectively diminish any such retinotopically driven adaptation effects by saturating the visual system and thus eliminating any differential stimulation across conditions.

Taken together then, the findings suggest that the orientation-selective adaptation effects we observed in the occipital-parietal pathway are related to higher-level shape processing. The shape processing in this pathway, however, does not appear to be concerned with establishing the object's identity or detailed geometry but rather with identifying its principal axis and thus its orientation. Other human neuroimaging studies have identified shape-sensitive regions within the posterior parietal cortex by contrasting activation to coherent shapes with activation to scrambled versions of those shapes (Dale et al., 2000; Denys et al., 2004; Faillenot et al., 1997; Grill-Spector et al., 1998, 1999; James et al.,

2002; Kraut et al., 1997). But it is important to remember that the shape-sensitive activity in the dorsal stream that was uncovered by this kind of contrast may also have reflected processing of the object's orientation rather than its identity. Such an interpretation would certainly be consistent with the findings of James et al. (2002) and Vuilleumier et al. (2002), who describe an area in the caudal part of the IPS that is sensitive to changes in the orientation of objects—even though they did not directly examine, as we did for area OPJ, whether or not the area is *selective* for changes in orientation.

Although the regions identified in earlier studies of the posterior parietal cortex have tended to be located in the most caudal parts of the IPS and extending into adjacent occipital areas, it is difficult to determine with any certainty how much overlap there is between these regions and area OPJ, which we identified using our adaptation paradigm. Area OPJ encompasses the junction of the intraparietal and transverse occipital sulci, anatomical landmarks commonly associated with the putative human homolog of monkey V3A, otherwise known as hV3A. Without retinotopic mapping (Tootell et al., 1997), however, no definitive conclusions can be drawn about the potential overlap of our identified area OPJ with hV3A. In fact, the most likely candidate for a functionally homologous region to OPJ in the macaque is an area in the lateral bank of caudal intraparietal sulcus (area c-IPS) that contains neurons that respond selectively to the three-dimensional features of an object (for review, see Sakata et al., 1998; Taira, Tsutsui, Jiang, Yara, & Sakata, 2000; Tsutsui, Sakata, Naganuma, & Taira, 2002). This area not only contains neurons that are tuned to the orientation of an object but it also sends projections to area AIP, an area that has been implicated in the visual control of grasping. Other investigators have also suggested that the regions in the caudal part of the human IPS (which may overlap with the region we are calling OPJ) might be homologous with area c-IPS and provide information about object orientation to human AIP (James et al., 2002; Shikata et al., 2001, 2003). If this is indeed the case, then it is perhaps not surprising that area OPJ shows orientation-specific adaptation effects. The putative homologies between human and monkey are not well established however and more research is required. For one thing, although the data are consistent with the claim that area OPJ plays an important role in the visual control of grasping, until an explicit comparison is made between the sensitivity of this region to changes in the orientation of graspable versus non-graspable objects, one cannot be certain that the activity in this region is related entirely to computing the orientation of objects for visuomotor control. It could be the case that area OPJ computes the spatial orientation of objects in general, and that its putative contribution to visuomotor control is only one of a number of different functions of this region (Ungerleider & Mishkin, 1982).

It is interesting to note that previous neuroimaging studies have described areas in the posterior parietal cortex in and around the IPS that show preferential activation to tools as compared to other classes of objects (e.g. Chao & Martin, 2000; Creem-Regehr & Lee, 2005; Johnson-Frey, 2004;

Okada et al., 2000). The sites of this activation were more anterior and dorsal than the area OPJ. Moreover, the tool-related activity in these studies was most evident in the left hemisphere, whereas our orientation-selective activation was in the right. But even so, the orientation of a tool has important implications for the pre-shaping of the grasping hand. It is possible that the activity in area OPJ provides information for tool-related computations in those posterior parietal areas that show differential activation to tools. Again, however, this will remain speculation until the appropriate experiments are carried out.

As discussed earlier, we identified an area in the right fusiform gyrus (area vTO) that appears to be highly selective for changes in object identity and is unaffected by changes in viewpoint. A number of investigators have reported similar findings. Some studies have found viewpoint-invariant regions in the fusiform gyrus and area LO of both hemispheres (Eger, Henson, Driver, & Dolan, 2004; James et al., 2002; Kourtzi, Erb, Grodd, & Bulthoff, 2003); others only in the left hemisphere (Vuilleumier et al., 2002). Other studies, however, have not found evidence for viewpoint-invariant processing anywhere in the fusiform, although they have found evidence for size- and position-invariance (Grill-Spector et al., 1999). The reasons for these discrepancies in the literature are not clear although the nature of the orientation change, the timing of events, and the deployment of attention may be important factors. In our experiment, the change in orientation was a mirror reversal, which like the change in orientation in the James et al. (2002) and Eger et al. (2004) studies, did not result in a foreshortening of the axis of elongation or any self-occlusion of object parts. In other words, the same object parts were visible (and to the same extent) across the change in orientation. This was not true in either the Vuilleumier et al. (2002) or Grill-Spector et al. (1999) study, where new object parts were revealed (and others occluded) when the object was rotated into the picture plane.

Another critical methodological feature of our experiment that set it apart from some of the other fMR-adaptation studies was the time scale of the repeating events. In our study, the repetition time, or repetition 'lag', was extremely rapid, with only a single intervening 'masking' stimulus. In the studies by James et al. (2002) and Vuilleumier et al. (2002), the repetition lag was long, often lasting many minutes, with many intervening stimuli. In the Eger et al. (2004) and Grill-Spector et al. (1999) studies the lag was similar to the one we used. Such methodological differences may lead to entirely different fMRI repetition effects, perhaps reflecting distinct underlying neural mechanisms (for review, see Henson, 2003). Whatever the mechanisms might be that underlie the different repetition-dependent effects that have been reported, the observed effects do not always map onto actual behavioral phenomena. For example, the faster reaction times associated with repeated presentation of the same eliciting stimulus are not paralleled by repetition-effects in early sensory areas, such as area V1, or in late motor areas such as M1 (for review, see Henson, 2003; and Henson &

Rugg, 2003). Conversely, despite the fact that we observed robust repetition effects for object orientation in the dorsal stream, a pathway that has been implicated in visuomotor control, there is no evidence for orientation-based behavioral priming in visually guided grasping tasks (Cant, Westwood, Valyear, & Goodale, 2005; Garofoanu, Kroliczak, Goodale, & Humphrey, 2004), presumably because the required coordinates for action are most effectively computed immediately before the movements are initiated, and as a consequence neither the coordinates for a particular action nor the resulting motor program need to be stored in memory. In short, there is an apparent inconsistency between the occurrence of fMR-adaptation in the dorsal stream and the absence of visuomotor priming. It is quite a different story in the ventral stream. Here the robust BOLD repetition-effects observed with object identity are paralleled by priming effects in a wide range of object recognition and discrimination tasks (e.g., James et al., 2002). Similarly, pharmacological manipulations have been shown to interfere with both fMR-adaptation effects in the ventral stream and behavioral priming (Thiel, Henson, Morris, Friston, & Dolan, 2001). All of this suggests that the repetition-effects observed in different brain areas and with different paradigms are unlikely to reflect the activity of a single mechanism, such as those invoked in models that talk about ‘suppression’ or ‘sharpening’ (e.g., Grill-Spector et al., 1999; for review, see Henson, 2003; Wiggs & Martin, 1998). Instead, the changes seen in different brain areas with stimulus repetition may arise for quite different reasons, and may or may not reflect repetition effects observed in behavior.

In conclusion, we have demonstrated differential sensitivity of the dorsal and ventral stream to object orientation and object identity, respectively. Such differential sensitivity (or processing biases) makes sense given the evolutionary divergence in the functions of the two streams. If the ventral stream is indeed involved in object recognition and goal selection then it is perhaps not surprising that it is sensitive to the identity of an object independent of the viewpoint from which it is seen. In contrast, if the dorsal stream is involved in the visual control of object-directed actions, then it might be expected to be more interested in the orientation of a potential goal object than its identity.

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