Ventral and Dorsal Visual Stream Contributions to the Perception of Object Shape and Object Location

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Abstract

■ Growing evidence suggests that the functional specialization of the two cortical visual pathways may not be as distinct as originally proposed. Here, we explore possible contributions of the dorsal "where/how" visual stream to shape perception and, conversely, contributions of the ventral "what" visual stream to location perception in human adults. Participants performed a shape detection task and a location detection task while undergoing fMRI. For shape detection, comparable BOLD activation in the ventral and dorsal visual streams was observed, and the magnitude of this activation was correlated with behavioral performance. For location detection, cortical activation was significantly stronger in the dorsal than ventral visual pathway and

INTRODUCTION

Extracting information about the shape and the location of visual information in the world around us is a fundamental function of the primate visual system. Interestingly, although shape and location perception appear to be seamlessly unified in our perception of a visual scene, neurophysiological evidence indicates that object properties, such as shape and texture, are processed by a temporal or ventral visual pathway, whereas the location or spatial position of the object is processed separately and independently by a parietal or dorsal pathway (Felleman & Van Essen, 1991; Desimone & Ungerleider, 1986; Desimone, Schein, Moran, & Ungerleider, 1985; Mishkin, Ungerleider, & Macko, 1983; Ungerleider, Galkin, & Mishkin, 1983). Findings from neuropsychological (e.g., Milner & Goodale, 1995; Goodale & Milner, 1992; Newcombe & Russell, 1969) and neuroimaging (e.g., James, Culham, Humphrey, Milner, & Goodale, 2003; Haxby et al., 1991, 1994) studies have confirmed this segregation of primary functions of the two pathways. We will refer to the specialization associated with a given pathway as the "primary" function of the associated areas.

More recently, several studies have challenged this strict segregation of primary functions, demonstrating that representations associated with shape and location

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did not correlate with the behavioral outcome. This asymmetry in cortical profile across tasks is particularly noteworthy given that the visual input was identical and that the tasks were matched for difficulty in performance. We confirmed the asymmetry in a subsequent psychophysical experiment in which participants detected changes in either object location or shape, while ignoring the other, task-irrelevant dimension. Detection of a location change was slowed by an irrelevant shape change matched for difficulty, but the reverse did not hold. We conclude that both ventral and dorsal visual streams contribute to shape perception, but that location processing appears to be essentially a function of the dorsal visual pathway.

processing are present in both visual streams (Sereno & Lehky, 2011; Kravitz, Kriegeskorte, & Baker, 2010; Konen & Kastner, 2008; Sereno & Maunsell, 1998). However, the functional implications of these distinct dorsal shape representations and ventral location representations, which we will call "nonprimary" functions (dorsal shape, ventral location), remain unclear. One possibility is that the activation of an area associated with a nonprimary function is non-task-related and has no apparent processing consequence for either shape or location processing per se. Alternatively, the nonprimary activation might play a functional role, in which case both visual streams would be engaged in both object identification and object localization (Jervis, Bennett, Thomas, Lim, & Castiello, 1999). Finally, there might be activation for a nonprimary function within a brain region, but this activation might reflect a subsidiary role: Thus, dorsal shape representations might exist solely to facilitate object localization or action, the assumed primary function of the dorsal stream; conversely, ventral location representations might exist solely to facilitate object identification, the assumed primary function of the ventral stream (Ganel & Goodale, 2003; Goodale & Humphrey, 1998; Goodale & Milner, 1992). Here, we adjudicate between these various hypotheses by exploring whether shape representations in the dorsal visual stream are functionally relevant to shape perception and, similarly, whether location representations in the ventral visual stream are functionally relevant to location perception.

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EXPERIMENT 1

Using functional imaging, we determine whether cortical activation in response to shape and location processing can be uncovered in each of the cortical pathways in the context of a perceptual task. First, we independently localized ROIs in each pathway in each participant. Then, in the experimental task (which we refer to as the "main task"), participants viewed two panels of objects presented simultaneously on a computer screen and indicated, in separate blocks, whether the panels differed either in terms of the shape of the depicted objects or in terms of their location. The shape change and location change detection tasks were matched behaviorally. Furthermore, the displays used were identical (only the instructions varied), and the patterns of eye fixations were monitored to make sure the two tasks were as similar as possible. As such, any differences in cortical activation cannot be ascribed to differences in the visual input, behavioral performance imbalances, or differences in shifts of attention or eye gaze. Therefore, any BOLD differences observed across the tasks are task specific and actively implicated in the service of either shape or location perception.

Participants

Eighteen adults (10 women, age range = 19–23 years) participated in the experiment. All were right-handed and had normal vision (corrected, if necessary). No participant had a history of neurological disorders, and all received monetary compensation for participation. Informed consent was obtained from all participants, and the Institutional Review Board of Carnegie Mellon University approved all procedures.

fMRI Acquisition

Participants were scanned in a Siemens (Erlangen, Germany) Verio 3T scanner with a 32-channel head coil. Functional images were acquired with an EPI sequence (repetition time = 2 sec, time to echo = 30 msec, flip angle = 79°, 3.2 mm isotropic voxels, field of view = $205 \times 205 \text{ mm}^2$, 36 transversal slices covering the whole brain). The 36 transverse slices were acquired in parallel using the Siemens protocol iPAT with an acceleration factor of 2 and 62 reference lines. An MP-RAGE sequence (1 mm³ voxels; 192 slices of size $256 \times 256 \text{ mm}^2$) was used for anatomical imaging.

Functional scans were slice scan time-corrected, motioncorrected, coregistered to their constituent anatomical image, normalized to Talairach space, and smoothed with a Gaussian kernel of 8.0 mm FWHM using BrainVoyager QX (Brain Innovations, Maastricht, The Netherlands). In addition, a two cycle, high-pass temporal filter (GLM with Fourier basis set) was applied before coregistration to remove linear trends. The experiment, implemented using E-prime 2.0 (Psychology Tools, Pittsburgh, PA), was run on a Windows XP-based PC. Stimuli were presented via an analog projector on a 20-in. screen (21° visual angle horizontally by 16° vertically at a distance of 100 cm away from the participants' eyes) situated at the bore opening of the MRI scanner at a resolution of 1024×768 (0.02° per pixel), 1-msec RT. Participants viewed the projection screen through a mirror attached to the head coil of the scanner. Eye movement data were collected using an infrared technique (Eye-Trac model 6, Applied Sciences, Bedford, MA).

Procedure

In a single 90-min session, participants completed eight functional runs: The first four runs constituted a shape and a location ROI localizer task (two runs per localizer), and the remaining four comprised shape and location change tasks (the main task).

Localizer Tasks

Participants completed two runs of each of the shape and location localizer tasks, with each comprising 10 blocks of trials (10 trials per block). The order of the localizer tasks was counterbalanced across participants.

Shape localizer. In the shape localizer task, adapted from Grill-Spector (2004), participants viewed two images of either whole or phase-scrambled objects displayed on either side of the screen center for 1.9 sec (see Figure 1A, B). On 20% of the trials (2 of 10 trials per block), the items matched, and participants indicated this by button press. Response was withheld on the nonmatching trials. On half the trials, the images appeared in a top left, bottom right configuration, and in the remaining half, in a top right, bottom left configuration. A block consisted entirely of whole object trials or scrambled object trials, and order was counterbalanced. Each block lasted for 22 sec and was preceded and directly followed by 8 sec of fixation. Trials were separated by 100 msec of fixation. At the beginning of each block, a dummy trial (presented for 1.9 sec) instructed participants as to the upcoming block.

Location localizer. This task, adapted from Haxby et al. (1991), contrasted distance matching (metric spatial representation), which is the key spatial process engaged in the main task (see below), with a position-matching task. On each trial, participants viewed a display with two panels containing a dot and a line, shown to either side of the screen center for 1.9 sec (Figure 1C, D). In separate, counterbalanced blocks, participants were required to perform either a distance-matching task (Figure 1C) or a side-matching task (Figure 1D), as

Figure 1. (A) A series of three sample trials from a whole-object matching block of the shape localizer, with fixation interspersed. The last trial depicts an object match. (B) A series of three sample trials from a scrambled-object matching block of the shape localizer, with fixation interspersed. The last trial depicts a scrambled-object match. (C) A series of three sample trials from a distance estimation block of the location localizer, interspersed with fixation. The last trial depicts a distance match between the ball and line across the two panels. (D) A series of three sample trials from a side-matching block of the location localizer, interspersed with fixation. The last trial depicts a match on the side of the ball, relative to the line, across the two panels.



instructed at the beginning of the block. The side- and distance-matching tasks were visually identical; thus, any BOLD differences are ascribed to regions associated with processes of spatial localization.

In a distance-matching block, participants compared the horizontal distance between the black dot and the vertical line across the two panels. This distance was the same in 2 of 10 trials, and participants indicated this by a button press (response withheld on different distances).

In a side-matching block, the horizontal distance between the black dot and the vertical line was always identical across the two panels, and participants determined whether the dot appeared on the same side of the line or not, irrespective of its vertical height (left or right; Figure 1D). In 2 of 10 trials, the dot position relative to the line was the same, and participants indicated this by a button press. On half the trials in a block, the panels appeared in a top left, bottom right configuration, and in the remaining half in a top right, bottom left configuration. In distance-matching blocks and in the nonmatch trials of the side-matching blocks, the two panels always depicted the dot at opposite horizontal and vertical positions; for example, if in one panel the dot was at the top left side of the line, in the other panel it would be presented at the bottom right side of the line. The distance between the dot and line at each of the four possible locations could

vary and was randomly drawn from a uniform distribution between 0 and 80 pixels, subject to the constraint that the distance was smaller than 30 pixels and greater than 18 pixels.

Main Task

This task was used to measure activation in response to shape and location discrimination. On each trial, participants compared two panels of objects, presented simultaneously on either side of the screen center, and reported whether they were the same or different either in their shape or location of the depicted objects (see below). Each panel consisted of a single object above a black horizontal line (Figure 2A). The line was 200 pixels wide (4°) and positioned so that its midpoint fell 300 pixels (6°) from the horizontal center of the screen. The two objects in the panels were always the same object (e.g., office chairs) but could differ between panels with respect to shape (e.g., two slightly different office chairs, see example in Figure 2B) or location (e.g., closer or further relative to the line, see example in Figure 2C). Twentytwo familiar objects, some man-made, some natural, some manipulable, and some not (Figure 2D; acquired from www.cnbc.cmu.edu/tarrlab/), were each rendered within a rectangle 186 pixels high \times 233 pixels wide (3.7° \times 4.7°; **Figure 2.** (A) Sample stimulus display of the main task of the fMRI work, consisting of two panels, each of which contains one object on top of a black horizontal line. (B) Sample stimulus display with a shape difference across the panels. (C) Sample stimulus display with a location difference in the panels. (D) All 22 objects used in the fMRI and psychophysical experiments.



average object size 2.3° visual angle; dimensions comparable with those used previously (Grill-Spector, 2004).

Across trials, the two panels appeared in one of two possible spatial configurations: on half the trials, panels appeared in a top left, bottom right configuration, and in the remaining half, in a top right, bottom left configuration. To preclude anticipation of the display layout, two distance parameters in the display were randomly varied across trials: object to line within a panel (25 pixels + 10-50 pixels) and edge-to-edge distance between panels (20-50 pixels). A location difference, if present, was induced by adding a maximum of eight more pixels to the vertical distance between one of the objects (randomly chosen) and its black line. All the distance constraints were implemented to ensure that the object images were confined within about 2° of visual angle so as to minimize the number of fixations.

When a difference between the panels was present, it was either easy or difficult to detect. Shape change detection difficulty was manipulated by creating three variants of each object: the central object (i.e., original image from database) was deformed along a shape dimension (e.g., thickness, width, roundness, etc.) in two opposite directions (by the same magnitude; Figure 3) to create two variants. The variant created by positively deforming (larger, wider, etc.) the central object was labeled as the "+1 object" and the variant created by negatively deforming (smaller, thinner, etc.) the central object was labeled as the "-1 object." A trial consisting of the central



Figure 3. The figure depicts how shape difference difficulty was manipulated. The central object was the original image obtained from the image database. It was deformed to create the +1 object by making the chair feet wider and the chair back rounder. The same central object was deformed to create the -1 object by making the chair feet narrower and the chair back less round, using adjustments of the same magnitude used to create the +1 object.

object and a variant (+1 or -1) constituted a difficult shape change detection, whereas a trial containing just the two extreme variants (+1 and -1) constituted an easy shape change detection, because it had twice the deformation magnitude of the difficult case.

The ease/difficulty of location judgments was controlled by varying the difference between the objects with respect to their distance from the line in each panel (e.g., the two office chairs relative to their respective horizontal lines). On the basis of pilot data, the easy and difficult levels of the location task were matched to the easy and difficult levels of the shape task in terms of inverse efficiency scores. Under the above behavioral matching, the number/pattern of eye fixations were also closely matched between the two tasks. The pilot study used for matching consisted of 10 participants (three women) who performed the tasks inside the inactive MRI scanner to emulate the MRI environment. For each participant and within each difficulty level (easy; difficult), the experiment program gradually adjusted the distance between the objects and lines in the location task, until the average inverse efficiency score matched that of shape within 100 msec. Three blocks of trials per condition were completed; the average of these three blocks was computed, compared against the average to be matched and adjustments made, if necessary. If accuracy was below 90% for a block, the block was repeated and the most recent average RT of that block was counted in the running average. As the final stimulus parameters were able to be matched across participants, the same stimulus parameters determined from this pilot session were used in the actual fMRI experiment without adjustment. The difficulty manipulation for shape and location change detections is included as a means of gauging activity related to attentional demands. The assumption is that increasing difficulty will affect activity (increase or decrease) in cortical regions associated with attentional demands (such as regions within the posterior parietal cortex). If difficulty level-related activity is comparable across the two tasks (no significant interaction between difficulty level and type of task), then we can assume that both tasks require comparable processing capacity or allocation of attention, and we would expect that activity to cancel out in the RFX contrasts mentioned below. The inverse efficiency score (expressed in milliseconds) is equal to the mean RT (for button press) divided by the proportion of correct responses, calculated separately for each condition and each participant. Lower values on this measure indicate better performance (Christie & Klein, 1995; Akhtar & Enns, 1989; Townsend & Ashby, 1983). Inverse efficiency scores discount possible speed-accuracy tradeoffs in performance and offer a single behavioral measure to be correlated with brain activity, leading to simpler and potentially more robust data analyses.

The trials were blocked by Task type and Difficulty level, forming a 2×2 factorial design. Critically, independent of condition, the same object images were presented

at the same on-screen locations. Each block consisted of 10 trials, separated by 100 msec of fixation. At the beginning of each block, participants were given instructions indicating the type (shape or location) but not the difficulty level of the block. Instructions were given via an additional, dummy trial presented for 1.9 sec at the beginning of the block: A display with exaggerated shape (larger deformation) or location differences was used to indicate the difference to be detected in the upcoming block. Participants were required to press a button if a difference was detected or to withhold response otherwise. In each block, 5 of the 10 trials were identical. Participants were not explicitly instructed on how to determine shape or location differences between panels but were shown multiple examples of each during the instructions section and during training. Participants were trained to criterion (90% accuracy) on 12 blocks (six blocks per task, three blocks per difficulty level) before scanning. A functional run of the main task consisted of twelve 22-sec blocks (10 trials per block), each preceded and followed by 8 sec of fixation.

Results

All imaging data were analyzed using BrainVoyager QX. Data from the localizer tasks were analyzed with repeated-measures random effects models (RFX GLMs). The resulting statistical maps were thresholded at q(FDR) < 0.05, using the false discovery rate approach for multiple comparisons correction (Genovese, Lazar, & Nichols, 2002). Data from the main task were analyzed using an RFX ANCOVA with Task type and Difficulty level as factors and were thresholded at q(FDR) < 0.01.

Shape Localizer

Statistical maps were created using the RFX contrast: [Whole objects > Scrambled objects] (Figure 4A). There was significant activation of lateral occipital cortex (LOC) and fusiform gyrus (FFG), bilaterally. Two masks were created from the activity of the selected regions (see Table 1), one from bilateral LOC and the other from bilateral FFG.

Location Localizer

Statistical maps were created using the RFX contrast: [Distance estimation > Side matching] (Figure 4B). A single mask, which served as the dorsal ROI, was created from all active regions between the most anterior (Talairach coordinates (x, y, z): 36, -36, 38; -36, -36, 38) and most posterior (Talairach coordinates (x, y, z): 23, -68, 24; -23, -68, 24) portions of the intraparietal sulcus (IPS), bilaterally (see Table 2 for all activated regions). The dorsal ROI consisted of 11,668 voxels (at the resolution of the structural data; MP-RAGE) and was comparable

Figure 4. (A) Cortical statistical map as revealed by the RFX contrast: [Whole objects > Scrambled objects] from the shape localizer. (B) Cortical statistical map as revealed by the RFX contrast: [Distance estimation > Side matching] from the location localizer.



Table 1. List of Regions Activated by the Shape Localizer Task

				Talairach		
Name of ROI	BA	t Score	No. of Voxels	x	у	z
1. Left hemisphere LOC	19	6.70	6890	-46	-73	-1
2. Left hemisphere FFG	20,36,37	8.17	6848	-35	-40	-16
3. Right hemisphere LOC	19	7.08	4117	44	-70	0
4. Right hemisphere FFG	20,36,37	5.41	3818	33	-36	-17

All regions activated by the contrast [Whole objects > Scrambled objects] during the shape localizer task are listed here and provided with Brodmann's areas (BA); *t* scores; size in number of voxels; coordinates defined by Talairach and Tournoux (1988) (*x*: left–right; *y*: anterior–posterior, origin in anterior commissure, *z*: inferior–superior). Two cortex masks were created from the activity in Regions 1, 3 and 2, 4, respectively, and were used to constrain the analyses of the shape and location change detection tasks (main task).

Table 2. List of Regions Activated by the Location Localizer Task

				Talairach		
Name of ROI	BA	t Score	No. of Voxels	x	у	z
1. EVC	17,18,19	16.38	50,628	-3	-78	2
2. Right hemisphere insular cortex	13	7.24	5893	31	19	8
3. Right hemisphere PPC	7	7.93	4931	23	-57	45
4. Medial SFG	6	6.45	4771	2	12	47
5. Left hemisphere PPC	7	6.50	3288	-25	-57	45
6. Left hemisphere insular cortex	13	6.24	2098	-29	19	6
7. Left hemisphere PrCG	6	6.10	653	-38	-11	45

All regions activated by the contrast [Distance estimation > Side matching] during the location localizer task are listed here and provided with Brodmann's areas (BA); *t* scores, size in number of voxels; Talairach coordinates defined by Talairach and Tournoux (1988) (*x*: left–right; *y*: anterior–posterior, origin in anterior commissure, *z*: inferior–superior). EVC = extrastriate visual cortex; PPC = posterior parietal cortex; PrCG = precentral gyrus; SFG = superior frontal gyrus. A cortex mask was created from the activity in Regions 3 and 5 and was used to constrain the analyses of the shape and location change detection tasks.

with the size of the shape localizer ROIs (LOC: 11,007 voxels; FFG: 10,666). The order of the RFX contrast ([Distance estimation > Side matching] vs. the reverse) was chosen based on (i) its similarity to the RFX contrasts used in the Haxby et al. (1991) experiments and (ii) preliminary data that indicated far stronger activation within the posterior parietal cortex for distance estimation compared with side matching. The above two reasons were also the basis for using distance estimation as the location-task portion of the main task.

Main Task: Behavioral Performance and Pattern of Eye Fixations

The shape and location change detection tasks were intended to elicit task-specific activation for shape and location processing, respectively. To infer task-specific activation, however, we first ensured that performance and eye movements (correlated with shifts of attention) did not differ across task.¹ To compare performance (inverse efficiency) for shape and location change detections, we conducted an ANOVA with Task type (Shape task vs. Location task) and Difficulty level (Easy vs. Difficult) as factors (Figure 5A). As expected, performance was lower for the Difficult than Easy trials, F(1, 68) =68.5, p < .01, equivalent so for the two types of Task, F(1, 68) = 0, p = .99. There were no statistical differences between Easy shape and Easy location change detections, p = .39, nor between Difficult shape and Difficult location change detections, p = .4. Despite the statistical equivalence of the means across Task within a Difficulty level, the interaction between the two factors reached significance, F(1, 68) = 3.04, p = .04. Pairwise comparisons (adjusted for multiple comparisons) revealed that the difficulty effect for shape (Difficult Shape – Easy Shape) was greater than for location, t(1, 1) 17) = 4.70, p (two-tailed) < .01. Raw RT and Accuracy values for all relevant conditions are also provided on Table 5.

The following procedure was used to compare the pattern of eve fixations between the two tasks: first Areas of Interest (AOIs) were constructed, corresponding to the areas on a stimulus display occupied by objects, and areas occupied by horizontal black lines and the space between them and the objects. The width of all AOIs was identical to the width of the objects (233 pixels, 4.7°). The height of the object AOIs was equal to the height of the objects (186 pixels, 3.7°) plus the maximum amount of vertical jitter possible (25 pixels, 0.5°), extending away from the screen center. The height of the line AOIs was chosen to be the maximum distance between a line and an object, with the vertical jitter and location difference gaps included (83 pixels). The line AOIs were then extended by 45 more pixels $(2.6^{\circ} \text{ total})$, either toward or away from the center of the screen, to account for any data (eye fixations) that might have occurred below the line when it was positioned at the furthest possible location away from an object. The above 45 pixels were the maximum possible extension of a line AOI before it overlapped with an object AOI below it.

Following the construction and placement of the AOIs, the number of eye fixations in each AOI for each Task type and Difficulty level were calculated for each participant. Eye fixations outside the designated AOIs were also calculated as a measure of noise (Figure 5B). Using the number of eye fixations as a dependent measure, an ANOVA was conducted with Task type, Difficulty level, and AOI (Object, Line, and Outside of Object or Line AOI) as factors. There was a significant main effect of AOI, F(2, 156) = 414.5, p < .001, but not of Difficulty level, F(1, 156) = 0.4, p = .53, or Task Type, F(1, 156) = 0.53,



Figure 5. The mean inverse efficiency scores (A) and number of fixations within each AOI (B) from the fMRI work are plotted for each Task type at each Difficulty level. Accuracy for each condition in (A) is displayed in brackets directly on top of each bar. Panel (B) depicts mean number of fixations per block of trials (10 trials). The error bars denote ± 1 *SE*.

p = .47. Pairwise comparisons on the AOI factor (adjusted for multiple comparisons) indicated that all AOIs were significantly different from each other, ps < .001. The vast majority of eye fixations (162; about four fixations per trial) occurred within the object AOIs, followed by fixations outside any AOI (52; about one fixation per trial). Only a small number of eye fixations (29; less than one fixation per trial) occurred within the line AOIs. More importantly, there were no significant interactions between any of the factors, indicating that participants fixated mostly on the object AOIs, irrespective of task performed or difficulty level.

Main Task: ROI-constrained Analysis

BOLD activity in response to Task type and Difficulty level was explored by constraining RFX ANCOVA analyses within the shape and location ROIs (separate analyses were performed for each localizer mask). Statistical maps for Task type were created using the RFX contrast [(Easy + Difficult shape task) > (Easy + Difficult location task)]. Statistical maps for Difficulty level were created using the RFX contrast [(Difficult shape task + Difficult location task) > (Easy shape task + Easy location task)].

Shape localizer ROIs. Within the shape localizer ROI masks, there was a significant effect of Task type but not of difficulty level, q(FDR) = 1, and there was no inter-

action between these factors, q(FDR) = 1. As anticipated, activation in response to shape change detections [Positive activation from the RFX contrast (Easy + Difficult shape task) > (Easy + Difficult location task)] was observed within the shape localizer mask. More importantly, however, in addition to this pattern of activation consistent with primary function, a region within the left hemisphere middle temporal gyrus, within the left hemisphere LOC cortex mask (BA 37; Talairach coordinates (x, y, z): -43, -69, 6), was active in response to location change detections [Negative activation from the RFX contrast (Easy + Difficult shape task) > (Easy + Difficult location task)] (Figure 6A).

Location localizer ROIs. Within the location localizer ROIs, there were significant effects of both Task type and Difficulty level but no interaction, q(FDR) = 1. As expected, activation in response to location change detections [Negative activation from the RFX contrast (Easy + Difficult shape task) > (Easy + Difficult location task)] was observed within the location localizer mask. Notably and of most relevance, in addition to this pattern of activation expected from primary function, shape change detections activated regions within bilateral posterior parietal cortex (Positive activation from the RFX contrast [(Easy + Difficult shape task) > (Easy + Difficult location task)] (BA 7 (superior parietal lobule); Talairach coordinates (x, y, z): 25, -56, 40; -28, -57, 42; Figure 6A).

In addition to the above pattern of activity related to Task type, regions within the location localizer ROIs bilaterally (BA 7 (superior parietal lobule); Talairach coordinates (x, y, z): 22, -60, 43; -26, -57, 43) were selectively more active during difficult change detections compared with easy change detections [Positive activation from the RFX contrast (Difficult shape task + Difficult location task) > (Easy shape task + Easy location task)] (Figure 6B). This increase in activation occurred irrespective of task performed (no interaction between Task type and Difficulty level). The general increase in brain activity within the location localizer ROIs presumably reflects the increasing attentional (i.e., processing capacity) demands across difficulty levels. Given that attentional demands are signaled by activation increases, the absence of a significant interaction between Task Type and Difficulty indicates the two tasks demand similar processing resources. It should further be noted that any brain activity related to these demands should have cancelled out in the RFX contrast [(Easy + Difficult shape

Figure 6. (A) Cortical statistical maps as revealed by the RFX contrasts: [(Easy + Difficult location task) > (Easy +Difficult shape task)] (bluegreen) and [(Easy + Difficult shape task) > (Easy + Difficult location task)] (orange-yellow) from the analyses on the shape and location change detection tasks of the fMRI work, constrained within the shape and location localizer cortex masks. The vellow outlines illustrate the brain regions that comprise the LOC cortex mask, the pink outlines illustrate the FFG cortex mask, and the green outlines illustrate the location localizer cortex mask. Purple outlines regions that showed significant correlations between the brain activity from the RFX contrast [Difficult shape task > Difficult location task] and the inverse efficiency scores from the Difficult shape task. (B) Cortical statistical maps as revealed by the RFX contrasts: [(Difficult shape + Difficult location task) > (Easy shape +Easy location task)] (blue) and [(Easy shape + Easy Location task) > (Difficult shape +Difficult location task)] (brown). The above contrasts represent Difficulty level in the analyses on the shape and location change detection tasks of the fMRI work, constrained within the shape and location localizer cortex masks. The yellow outlines illustrate the LOC cortex mask, the pink outlines illustrate the FFG cortex mask, and the green outlines illustrate the location localizer cortex mask.



Figure 7. Mean BETA value per $3 \times 3 \times 3$ voxel cube centered around the most active voxel and anatomical midpoints between the most active voxels per participant. An illustration of two of the three midpoint ROIs is shown on Figure 7 next to the bars. The RFX contrasts [(Easy + Difficult location task) > (Easy + Difficult shape task)] and [(Easy + Difficult shape task) > (Easy + Difficultlocation task)] are plotted for bilateral IPS, bilateral LOC, bilateral IPS midpoint, and left hemisphere LOC midpoint (the right hemisphere LOC did not have any location change activity for us to define a midpoint cube). The ROIs used were obtained from the localizer tasks and are the same ROIs used as cortex masks for the ROI constrained analyses. The error bars denote ± 1 SE.



task) > (Easy + Difficult location task)] used in our previous analyses.

Comparison between ventral and dorsal ROIs on task type. Thus far, the analyses show that shape and location processing elicit activity in both ventral and dorsal ROIs but do not provide insights into how the magnitude of the shape and location related activity compares in each ROI and across ROIs. To compare directly the magnitude and pattern of activity between the ventral and dorsal ROIs, in response to Task type, we used the group bilateral LOC and IPS ROIs (obtained from the localizer tasks) to identify the voxels with the most positive activity (in each ROI) in response to the RFX contrasts [(Easy + Difficult shape task) > (Easy + Difficult location task)and its reverse [(Easy + Difficult location task) > (Easy +Difficult shape task)], separately for each participant. Note that both contrasts above provide both positive and negative activation, with negative activation essentially being the reverse of the current contrast. Two contrasts were used so that only positive activation would be obtained, corresponding to either shape or location change detections (within each ROI; LOC and IPS ROIs) for ease of comparison. We then expanded $3 \times 3 \times 3$ voxel cubes (9.6 mm^3) ; at the resolution of the functional data) around the most active voxels obtained above (one cube per RFX contrast so we could sample both shape and location related activity from each ROI) and averaged the activity within each cube, in terms of BETA values, to obtain a single BETA value average for each cube. Each cube consisted of about one third of the active region it was sampling within an ROI. The size of the cube was selected

to minimize overlap between the active regions from each contrast within each ROI. In addition to the above, peak-centered ROIs, using the RFX contrast [(Easy + Diffi-(cult shape task) > (Easy + Difficult location task) from the group level ROI analysis, we created $3 \times 3 \times 3$ voxel cubical ROIs centered on the anatomical midpoints between the positive and negative peak activity voxels in left and right hemisphere IPS and left hemisphere LOC (as defined by the localizer tasks; one midpoint ROI was placed at every location where a subarea existed between positive and negative activity from the contrast mentioned above; see Figure 7). The midpoint ROIs were used to sample activity from the regions separating the shape and location activity peaks within each ROI, separately for each participant, as a means of measuring the degree of segregation between the main shape and location activity within each ROI across participants (Figure 7). The hypothesis is that if the shape and location peaks are anatomically segregated across participants, then very little activity should be observed within the midpoint ROIs. The average BETA values from each ROI were then entered into a repeated-measures ANOVA with ROI (bilateral LOC, bilateral IPS, left hemisphere LOC midpoint [right hemisphere LOC did not have any location activity], bilateral IPS midpoint) and RFX Contrast (positive activation from [(Easy + Difficult shape task) >(Easy + Difficult location task)] versus positive activation from [(Easy + Difficult location task) > (Easy + Difficult shape task)]) as factors (Figure 7). ROI was the only significant main effect, F(3, 136) = 17.5, p < .01. RFX contrast (shape task vs. location task), F(1, 136) = 2.4, p = .13, was not statistically significant but there was a

significant interaction between these two factors, F(3, 136) = 10.15, p < .01. Pairwise comparisons (adjusted for multiple comparisons) were then conducted to explore the significant interaction between ROI and RFX Contrast.

The pairwise comparisons show four critical results: (i) Within bilateral IPS, activity in response to the nonprimary shape change detections (positive activity from [(Easy + Difficult shape task) > (Easy + Difficult location task)]) was not statistically different from activity in response to the primary, location change detections (positive activity from [(Easy + Difficult location task) >(Easy + Difficult shape task)]), p = .38, indicating that the strength of the BOLD signal was equivalent in the dorsal stream (within the location localizer ROI) for shape and location discriminations. In contrast, within bilateral LOC, activity in response to the primary, shape change detections (positive activity from [(Easy + Difficult shape)]task) > (Easy + Difficult location task)]) was significantly stronger compared with activity in response to the nonprimary, location change detections (positive activity from [(Easy + Difficult location task) > (Easy + Difficult shape)task)]), p < .01 (Figure 7). (ii) Within bilateral IPS, activity in response to shape and location change detections was equivalent to activity in response to shape change detections within bilateral LOC, ps = .13. That is, shape change detections led to comparable activation levels in both ventral and dorsal (nonprimary) visual streams. In addition, dorsal activity in response to location change detections was comparable in magnitude to ventral activity in response to shape change detections; thus, the two visual streams appear to be comparably active in response to their primary task domain. (iii) Activity in response to location change detections in bilateral LOC, the nonprimary activity, was significantly weaker compared with activity in response to the expected location change detections in bilateral IPS, p < .01. Although shape change detections activated both visual streams comparably, location change detections activated dorsal cortex significantly more strongly than ventral cortex. (iv) Midpoint ROIs were equally active for shape and location change detections, ps = .6 (as expected), and this overall activity was significantly weaker compared with the activity obtained from the peak-centered ROIs, p < .01. More importantly, within bilateral IPS (as defined by the location-localizer task) there was a substantial decrease in activity between peak and midpoint ROIs for both shape and location change detection activity (shape change activity, p = .04; location change activity, p < .01). This drop of activity for both tasks suggests the presence of two anatomically distinct peaks of comparable magnitude in IPS, each corresponding to one task type. The same was not true for LOC. Although the primary shape change detection activity within LOC decreased within the midpoint cube ROI relative to the peak cube ROI, p < .01, the nonprimary location change activity did not, p = .98, and it was overall comparably weak (in relation to the primary

shape activity), both at the peak and midpoint ROI. This pattern of activity within LOC suggests a single activity peak, corresponding to shape change detections and a weak, relatively uniform activity corresponding to location change detections that becomes significant because of the drop of the primary shape activity a small distance away from the peak. In short, regions within IPS appear to respond to both shape and location change detections, whereas regions within LOC appear to be responsive mostly for shape change detections.

These findings suggest a striking asymmetry between the dorsal and ventral streams with respect to nonprimary functionality. Activation was comparable across the dorsal and ventral areas with respect to primary functions. In addition, dorsal activation was comparable in response to detection of location (primary) and shape (nonprimary) changes. However, ventral activity was significantly stronger for shape processing, the primary function, than for location, the nonprimary function.²

Main Task: Whole-brain Analysis

An examination of the pattern of data across the entire cortex, without ROI constraint, revealed a significant main effect of Task type, but not of Difficulty level, q(FDR) = 0.1, and there was no interaction between these factors, q(FDR) = 1. Statistical maps for Task type were created using the same RFX contrasts as in the ROI constrained analyses (Figure 8A), and the activated brain regions are shown in Table 3.

Task type. Consistent with the findings of the ROI constrained analyses and as expected from the primary functions of ventral versus dorsal areas, shape change detections (positive activation from the RFX contrast [(Easy + Difficult shape task) > (Easy + Difficult location)task)]) activated several regions within the inferior temporal cortex, and location change detections (negative activation from the RFX contrast [(Easy + Difficult shape task > (Easy + Difficult location task)) activated several regions within the posterior parietal cortex, bilaterally. Also, in agreement with the ROI analyses, certain regions within the posterior portion of the parietal lobes, bilaterally, were active during shape change detections (positive activation from the RFX contrast [(Easy + Difficult shape task) > (Easy + Difficult location task)]), and similarly, regions within the right hemisphere LOC and left hemisphere middle temporal gyrus (MTG) were active during location change detections (negative activation from the RFX contrast [(Easy + Difficult shape task) > (Easy +Difficult location task)]).

Brain-Behavior Correlations

In both the ROI-constrained and whole-brain analyses, shape and location change detections lead to cortical activation in both ventral and dorsal visual streams. The Figure 8. (A) Cortical statistical maps as revealed by the RFX contrasts: [(Easy shape task + Difficult shape task) > (Easy location task + Difficult location task)] (orange-yellow) and [(Easy location task + Difficult location task) > (Easy shapetask + Difficult shape task)] (blue-green) from the shape and location change detection tasks of the fMRI work. Details of activated regions are given in Table 3. (B) Cortical statistical maps as revealed by the RFX contrasts in (A). The panel on the left depicts the statistical map at a threshold of $p < 3 \times$ 10^{-6} , the highest threshold at which activation in response to location change detections was still observable in the temporal cortex. The panel on the right depicts the same map at a more conservative threshold of $p < 4.3 \times 10^{-8}$, the highest threshold at which activation in response to shape change detections was still observable in the posterior parietal cortex.



ventral stream activity in response to location change detections, however, appears to be weaker than the dorsal stream activity in response to shape change detections. Notably and critically, this asymmetric pattern of activation across the ventral and dorsal visual streams is task specific and not a result of the object images presented, their overall locations on the screen, or a difficulty imbalance between the two tasks. What remains to be determined is whether these patterns of activation are functionally relevant to shape and location perception per se. Accordingly in this next analysis, we correlated the activity from the ROI-constrained analyses with the individual's behavioral performance (using inverse efficiency scores).

Four RFX contrasts were created to represent each level of the factorial design of the main task (Table 4). Statistical parametric maps of brain activity, from the four RFX contrasts depicted in Table 4, were then obtained separately for each participant. For each of the four contrasts, an RFX ANCOVA was run with four covariates consisting of the inverse efficiency scores of the participants for each one of the four levels of the factorial design. The statistical maps resulting from the brain activity–behavior correlations were thresholded at q(FDR) < 0.05. The RFX ANCOVA analyses used in the brain activity–behavior correlations were all constrained within the ROIs identified by the shape and location localizer tasks (separate analysis were run for each ROI).

The above analysis yielded significant BOLD-inverse efficiency correlations in the left LOC, r(of most significant voxel) = .70, and the left IPS, r(of most significant voxel) = .76, only. The significant correlations were between the RFX contrast [Difficult shape > Difficult location] and inverse efficiency scores from difficult shape change detection trials (Figure 9 and purple outlines in Figure 6A). Brain activity in response to location change detections did not correlate with behavior in any of the localized regions (cortex masks). No significant brain activity–behavior correlations were found in the FFG cortex mask.

EXPERIMENT 2

Our fMRI study indicates that detection of location and shape change processing is common to dorsal brain regions. This raises the question of whether the processing of shape and processing of location information engage separate, independent processes. This hypothesis predicts that irrelevant variations in one feature should

				Talairach		
Name of ROI	BA	t Score	No. of Voxels	x	у	z
1. Left hemisphere ITC	17–20,35,37	7.69	53,685	-29	-73	-7
2. Right hemisphere ITC	18–20,37	10.5	45,172	31	-73	-10
3. Left hemisphere MFG	9	6.79	6615	-38	10	25
4. Right hemisphere MFG	46	5.30	6485	45	21	26
5. Left hemisphere PPC	39	4.64	2333	-28	-62	36
6. Right hemisphere PPC	19	3.74	1413	28	-61	37
7. Medial SFG	6	4.8	638	-4	6	49
8. Left hemisphere perirhinal cortex	36	5.51	571	-29	-1	-28
1. Right hemisphere PPC	7	7.87	13429	12	-60	54
2. Left hemisphere PPC	7	6.12	7928	-15	-62	51
3. Right hemisphere postcentral gyrus	6	5.66	4013	22	-7	53
4. Left hemisphere PsCG	6	3.7	2317	-24	-8	48
5. Left hemisphere MTG	39	5.75	2125	-43	-71	18
6. Right hemisphere LOC	19	5.10	1858	35	-77	23
7. Left hemisphere lingual gyrus	18	4.92	1308	-10	-79	-12

Table 3. List of Regions Activated by the Main Task (Shape and Location Processing Tasks) of the fMRI Work

All regions activated by the contrasts [(Easy shape task + Difficult shape task) > (Easy location task + Difficult location task)] (orange) and [(Easy location task + Difficult location task) > (Easy shape task + Difficult shape task)] (blue) during the main task of the experiment are listed here and provided with Brodmann's areas (BA); *t* scores; size in number of voxels; coordinates defined by Talairach and Tournoux (1988) (*x*: left-right; *y*: anterior-posterior, origin in anterior commissure, *z*: inferior-superior). ITC = inferior temporal cortex; MFG = middle frontal gyrus; MTG = middle temporal gyrus; PPC = posterior parietal cortex; PSCG = postcentral gyrus; SFG = superior frontal gyrus.

have no impact on judgments about the other. Accordingly, we investigated whether task-irrelevant differences in shape affected performance in location judgments, and vice versa. Such a task-irrelevant difference will be termed a "distracter." The independence hypothesis predicts no interference from task-irrelevant distracters; conversely, distracter effects would indicate interdependence between shape and location processes.

Participants viewed displays similar to those adopted in the fMRI studies. On each trial, two panels, each comprising two objects placed near a horizontal reference line, were shown, one on each side of fixation (see Figure 10A, B). The pairs could be identical or could have one or two differences in object shape and/or object location. In separate, counterbalanced blocks, participants indicated the number of shape differences only or location differences only (ignoring the other dimension). This blocking was intended to engage only the shape or location mechanism, respectively, making differences on the alternative stimulus attribute clearly orthogonal to the participant's task and reducing possible interference from the nonrelevant channel. Importantly, using the two-object panel arrangement, albeit more complex than the single-object panel arrangement of the fMRI experiments, we ensured that the nontarget changes would be as visually separate and as much in the background as possible. Given these constraints, this two-object panel design provides a strong test of whether or not participants could ignore the nontarget

Table 4. List of the RFX Contrasts Used in the BOLD-inverse Efficiency	Correlation	Analysis
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	Dif	ficulty Level
Task Type Easy		Difficult
Shape	RFX contrast: [Easy shape > Easy location]	RFX contrast: [Difficult shape > Difficult location]
Location	RFX contrast: [Easy location > Easy shape]	RFX contrast: [Difficult location > Difficult shape]

Four RFX contrasts represent each of the four levels of the factorial design of the main task of the fMRI work. Brain activity from each of the four RFX contrasts depicted was correlated with the participants' inverse efficiency scores obtained for each one of the four levels of the factorial design of the experiment.

Figure 9. Cortical statistical maps as revealed by the RFX ANCOVA correlation analyses between the RFX contrast [Difficult shape > Difficult location task] and inverse efficiency scores from difficult shape change detections (red) constrained within the shape and location localizer cortex masks. Blue outlines indicate regions that were active in the RFX contrast [(Easy + Difficult location task) > (Easy + Difficultshape task)]. Orange outlines indicate regions active in the RFX contrast [(Easy + Difficult shape task) > (Easy + Difficult location task)]. Yellow outlines illustrate the LOC cortex mask, and green outlines illustrate the location localizer cortex mask.



changes. In addition, the above design allowed for shape and location changes to occur in a single trial on separate pairs of objects (only one difference was possible per pair of objects across panels). As a result, participants could not respond based on the presence of a nontarget stimulus alone (which could convert the nontarget stimuli into potential targets), allowing us to explore the effects of the nontarget stimuli as distracters per se.

Figure 10. (A) Sample stimulus display from the behavioral work. Each panel contained two objects separated by a black horizontal line. The rows of the two panels always matched with respect to the type of objects depicted, although the corresponding objects themselves could differ. (B) Sample stimulus display with two differences in the corresponding objects, one in location and one in shape. (C) Sample stimulus display with one shape difference between the pairs. (D) Sample stimulus display with two shape differences between the pairs. (E) Sample stimulus display with two differences between the pairs, one shape and one location.



Participants

Twenty-five right-handed undergraduate Carnegie Mellon University students (14 women, between 20 and 24 years) with normal vision (corrected if necessary) received course credit for participation. None of these participants completed Experiment 1.

Methods

Apparatus and Stimuli

The experiment, implemented using E-prime 2.0, was run on a Windows XP-based PC with a 22-in. $(33.4^{\circ}$ horizontal $\times 22^{\circ}$ vertical at a distance of 80 cm away from the participants' eyes), 3-msec RT computer display at a resolution of 1680 \times 1050 pixels (0.02° per pixel). Each image comprised two side-by-side panels, each containing two objects (e.g., a flask and a detergent bottle), separated by a black horizontal line (see Figure 10A). The objects in the same row ("corresponding objects") could differ across panels with respect to shape (e.g., two different flasks) and/or location (e.g., closer or further relative to the line, see example in Figure 10B). The objects, each rendered 150 pixels high (3°) \times 188 pixels wide (3.8°), were identical to those used in the imaging study (Figure 2D shows all the objects in the experiment).

Each horizontal line in the display was 400 pixels wide and positioned so that the midpoint fell 300 pixels to the left and right of the horizontal center of the screen for each panel. Within each panel, on each trial, the vertical distance between each of the two objects and the black line was randomly drawn from a uniform distribution between 0 and 50 pixels, subject to the constraint that the distances of the top and bottom objects from the line were not identical.

On each display, the panels could be identical or could show one difference between two corresponding objects (shape or location), two differences of the same type, or one shape and one location difference (Figure 10C–E). In the last two cases, only one difference could be present per pair of corresponding objects across panels (i.e., a pair of corresponding objects across panels could not differ with respect to both shape and location).

When a difference between two corresponding objects was present, it could be either easy or difficult to detect. Shape and location difficulty were manipulated in the same way as in the fMRI work. On the basis of pilot data, the easy and difficult levels of the location task were matched to the easy and difficult levels of the shape task in terms of inverse efficiency scores (RT/accuracy). This matching was achieved by using a vertical distance difference of 25 and 18 pixels for the easy and difficult location discriminations, respectively. These parameters were determined by a pilot study using the same procedure as the pilot in Experiment 1 (see above), but with seven participants (two female) who performed the tasks on the same computer and screen used in the actual experiment. The difficulty manipulation was included to explore whether the interdependence of shape and location is independent of the salience of the signal from the distracter attribute (Table 5).

Procedure

Participants sat in a well-lit room 80 cm away from the display screen and were given both spoken and written instructions, along with examples of shape and location differences at both levels of difficulty. Two blocks of trials were run. At the beginning of each block, participants were given a rule instructing them to search for either location difference/s only or shape difference/s only. Rule was thus an independent variable with two levels (Rshape or Rlocation), which were blocked in a counterbalanced order across participants. Given a rule, one type of difference would become the target (e.g., shape under Rshape), and the other type would become a task-irrelevant, distracter difference (e.g., location differences under Rshape).

Each trial consisted of a fixation cross, presented for 600 msec, followed by the presentation of the two panels of objects. Participants were required to compare the two panels and to indicate the total number of differences (according to the rule they were given) between them, using a numeric keypad and the keys "0" (no differences, identical panels), "1" (single target difference present), and "2" (two target differences present). The stimuli remained present until response, but participants were instructed to respond as quickly and as accurately as possible. Following the response, a 500-msec feedback display was presented for incorrect trials. RT and accuracy (used to derive inverse efficiency scores) were measured as a function of the number of differences between panels (0, 1, 2), difference type if any (shape, location),

Table 5. List of Average RT, Accuracy, and Inverse Efficiency Scores for Each Condition Used in Experiment 1

	RT (msec)		Accuracy (%)		Inverse Efficiency (msec)			
Task Type	Difficulty Level							
	Easy	Difficult	Easy	Difficult	Easy	Difficult		
Shape change detection	1037	1209	100%	88%	1038	1376		
Location change detection	1090	1206	98%	93%	1118	1298		

	RT (msec)		Accuracy (%)		Inverse Efficiency (msec)	
				Rule		
Type of Trial	Rshape	Rlocation	Rshape	Rlocation	Rshape	Rlocation
No distracter (or target)	2368	2197	96.5	86.7	2469	2592
Single easy target	2335	2280	86.2	80.1	2759	3068
Single difficult target	2623	2500	68.1	73.2	4147	4076
Two easy targets	2265	2160	82.4	78.6	3244	2827
One easy and one difficult target	2575	2448	61.2	67.9	4928	3751
Two difficult targets	2909	2696	49.6	60.4	7346	4864
Single easy distracter	2381	2709	97.9	80.1	2441	3460
Single difficult distracter	2328	2442	95.2	80.1	2439	3169

Table 6. List of Average RT, Accuracy, and Inverse Efficiency Scores for Each Condition Used in Experiment 2

rule (Rshape, RLocation), and difficulty level of the difference (easy, difficult). Participants were exposed to all independent variables in a within-subject design. Within each block, all conditions, defined by number, type of differences, and difficulty, had the same number of trials. Within a block, object pairs were selected randomly from the database of 22 object triples, without replacement. Once all 22 objects were presented, the sampling list was reset, and this process was repeated. The two blocks were separated by a 2-min break. Before the experiment, participants completed a training session consisting of a single presentation of each possible level of the independent variables across the two rule types using all 22 objects. If more than six errors occurred during the training, it was repeated.

Results

In this behavioral part of our work, repeated-measures general linear models were used to analyze all data, with p < .05, unless adjustments for multiple comparisons were needed. All multiple comparisons used Sidak corrections. The main dependent variable of Experiment 2, similar to the fMRI experiment, is inverse efficiency (defined as RT/Accuracy). The raw RT and Accuracy values for all relevant conditions are also provided on Table 6.

Analysis of Trials with Target Differences Only

To test whether the inverse efficiency scores for processing location and shape identity were comparable, analyses with Rule (Rshape vs. Rlocation) as a factor were conducted separately for trials with one target difference or two target differences only. Note that these analyses only incorporate trials with no distracters (i.e., no taskirrelevant differences).

To test the effect of a single difference on the target attribute (e.g., a location difference under Rlocation or

a shape difference under RShape), the analysis included factors Rule and Target Status (Identical, i.e., no target or distracter differences, Single Easy Difference or Single Difficult Difference). Target Status was the only significant main effect, F(2, 23) = 28.69, p < .01 (Figure 11A). Pairwise comparisons (adjusted for multiple comparisons) showed that responses to an easy-to-detect difference were faster than to a difficult-to-detect difference, p < .01. Furthermore, trials with identical pairs were faster to detect compared with both an easy-to-detect difference, p = .02, and a difficult-to-detect difference, p < .01. Importantly, neither the effect of Rule, F(1, 24) = 0.28, p = .60, nor the interaction between Rule and Target Status, F(2, 23) = 0.29, p = .65, were significant.

To test the effects of two differences on the target attribute, the analysis included the factors Rule and Target Status (Identical, $2 \times \text{Easy Differences}$, $2 \times \text{Dif-}$ ficult Differences, $1 \times \text{Easy}$, and $1 \times \text{Difficult Difference}$). Target Status and Rule were both significant main effects, F(3, 22) = 21.1, p < .01; F(1, 24) = 6.34, p = .02. The Rule effect indicated that under Rshape participants responded more slowly than under Rlocation (Rshape, 5173 msec; Rlocation, 3814 msec). As such, Rshape and Rocation are not matched in terms of inverse efficiency scores in trials with two target differences present. In contrast, Rshape and Rlocation appear to be closely matched in trials when there is a single difference between the pairs. Accordingly, in subsequent analyses, to test the main experimental hypotheses concerning distracter effects, only data from trials where there is a single difference on the distracter rule are considered.

Effects of a Single Distracter (Irrelevant Difference) on Rshape and Rlocation Identity Matching

The second set of analyses evaluated the effects of a single difference in the distracter rule on trials where the corresponding object stimuli were identical on the



Figure 11. (A) Mean inverse efficiency scores (in msec) plotted for Rshape and Rlocation in trials of the behavioral work with identical pairs (No targets or distracters), a single easy target differences or a single difficult target difference. Accuracy for each condition is displayed in brackets directly on top of each bar. The error bars denote ± 1 *SE*. (B) Mean inverse efficiency scores (in msec) for each rule (Rshape, Rlocation) on trials with a distracter difference or no difference only, as defined by Distracter Status: No distracter (or target), Single Easy Distracter, or Single Difficult Distracter. Accuracy for each condition is displayed in brackets directly on top of each bar. The error bars denote ± 1 *SE*.

target rule (see Figure 11B). The analysis included the factors Rule (Rshape or Rlocation) and Distracter Status (No distracter, a Single Easy Distracter, or a Single Difficult Distracter—the latter two constituted irrelevant differences that were easy or difficult to detect, respectively). Correct responses in trials under all levels of the Distracter Status factor required participants to press the "0" key, indicating that the object pairs were identical with respect to the target rule.

There were significant main effects of both Rule and Distracter Status, F(1, 24) = 9.47, p < .01; F(2, 23) = 9.2, p < .01, as well as an interaction, F(2, 23) = 4.45, p = .02. The interaction was pursued with follow-up analyses at each level of Rule with Distracter Status as the sole factor. In the analysis of Rshape, Distracter Status was not a significant main effect, F(2, 23) = 0.05, p = .95, indicating that a single location difference, whether easy or difficult, does not affect performance when participants search for a shape difference. In contrast, the Distracter Status effect was significant under Rlocation, F(2, 23) = 6.9, p < .01. Pairwise comparisons indicated that Rlocation trials with no distracter present were significantly faster than trials with a single shape distracter, whether easy or difficult, ps = .04 (Figure 11B).

In summary, a single distracter (irrelevant difference) affected inverse efficiency scores in an asymmetric pattern: Whereas a location distracter had no effect on the time to match targets on shape, a shape distracter slowed the matching of targets on location. The effect of shape on location was independent of the salience of the distracter content, as manipulated by the level of difficulty.

These results implicate a component of shape processing when the primary task is location processing.

GENERAL DISCUSSION

Converging evidence from several studies shows that shape and location representations exist in both the dorsal and ventral visual streams (Sereno & Lehky, 2011; Kravitz et al., 2010; Konen & Kastner, 2008; Sereno & Maunsell, 1998). However, the functional implications of these cross-stream shape and location representations remain unclear. Here, we demonstrated similar commonality of activation in a novel change detection task and then explored whether activation in response to shape changes in the dorsal visual stream were functionally relevant for shape perception and, similarly, whether activation in response to location changes in the ventral visual stream are functionally relevant for location perception.

The three most critical aspects of the fMRI work were as follows. First, in accord with earlier studies (James et al., 2003; Marois, Leung, & Gore, 2000; Goodale & Milner, 1992; Haxby et al., 1991; Ungerleider & Mishkin, 1982), robust activation in response to shape change detections was observed in the ventral visual stream and, similarly, robust activation in response to location change detections was observed in the dorsal visual stream. This pattern confirms the primary functions of those areas. Second, nonprimary activation was observed in the dorsal visual stream in response to shape change detections and in the ventral stream in response to location change detections. Furthermore, both ventral and dorsal stream activity in response to shape change detections correlated significantly with behavioral performance.

Third, there was an asymmetry in the nonprimary activation, in that dorsal activity in response to object matching was more robust than ventral activity in response to object localization. In addition, there was a positive correlation between BOLD responses and inverse efficiency in dorsal stream activity for shape change detections, but not in the ventral stream for location change detections.

Finally, an analysis of activation between ROIs suggested that there are distinct focal regions for shape and location processing in the dorsal stream (within the regions identified by the distance estimation localizer task). In essence, regions that were active in response to distance estimation, as observed by the distance estimation localizer task, under the main task, split into two subsections with one responding more to shape and the other more to location. In contrast to the above observation, the ventral stream pattern suggests a focal region for shape but a more diffused and relatively weak processing for location (compared with shape activity in the same ROIs). The functional implications of these intriguing findings remain to be investigated.

Given that the shape and location change detections were matched behaviorally for performance at a given level of difficulty and that the visual inputs were identical for both tasks, an account of the results in terms of differential task demands or differential eye movement patterns is not viable. The observed activation pattern is thus assumed to be task specific: in the service of the shape and location change detections engaged in each task.

These findings suggest that shape identification is mediated by both ventral and dorsal visual streams, whereas location perception appears to be a more exclusive function of the dorsal visual stream. These fMRI results complement and extend the findings of earlier studies (e.g., Konen & Kastner, 2008) by providing evidence that the previously identified dorsal shape representations contribute functionally to shape perception. In addition, our results indicate that, with respect to shape processing, the two visual streams may not be as strictly independent in their function as originally assumed (e.g., James et al., 2003; Milner & Goodale, 1995; Haxby et al., 1991, 1994; Goodale & Milner, 1992; Newcombe & Russell, 1969).

The fMRI-based inference, that shape perception is subserved by both visual streams whereas location perception is essentially a function of the dorsal visual pathway, is bolstered by findings from our separate psychophysical investigation. When the participant's task was to detect location differences between corresponding objects relative to a reference line, irrelevant variations in the shape of the objects slowed performance. Trials with fully identical pairs in a location-matching task were faster than trials with a single, task-irrelevant shape difference. In contrast with this interference from irrelevant shape differences on location processing, no corresponding effect of a location difference on shape matching was obtained. Notably and critically, this asymmetric interference pattern across shape and location was observed under the constraint that the two dimensions were matched a priori for difficulty of processing.

The findings of the behavioral investigation contrast with results of other studies, which indicate no interference between shape and location processing (at the level of the ventral and dorsal visual streams, e.g., Irwin & Brockmole, 2004; Müller & Rabbitt, 1989). This difference presumably reflects the intensive perceptual demands of our task, as indicated by the mean RTs on the order of 2.5 sec (cf. approximately 0.5 sec in Irwin & Brockmole, 2004).

Furthermore, to our knowledge, our behavioral study is the first to provide evidence for interference of shape information on location processing, within the visual domain, without either imposing a working memory load (thus tapping relatively late processes; see Wood, 2011; Chan & Newell, 2008) or using a reach/grasp response (involving the action system as well as perception; see Jervis et al., 1999). Our findings are also in agreement with studies performed outside the visual domain. One example would be the study by Tardif, Spierer, Clarke, and Murray (2008) in which the authors demonstrate interactions between the auditory "what" and "where" pathways and produce evidence that is consistent with that we offer in this study.

The two components of our investigation converge to indicate shared resources for processing location and shape. The brain imaging data reveals that regions in the dorsal stream contribute functionally to both location and shape processing and our behavioral data further indicate that the presence of a shape difference diverts resources from location comparisons. Collectively these results suggest that brain areas that serve the primary "where/how" function of the dorsal stream are recruited to process shape. Moreover, the recruitment appears to be outside of attentional control, as in our behavioral work, not only is location processing sensitive to inputs from object-based processes, but it also cannot filter out these inputs.

In contrast, these studies provide little evidence that object-based processes contribute to the processing of spatial relations among discrete objects (i.e., their relative spatial location within a visual scene). Although nonprimary location areas were identified in the ventral stream, they were, as noted above, weaker than nonprimary shape areas and not directly implicated in performance. Moreover, location distracters failed to affect shape comparisons.

Although the present results point to the possibility that some aspect of location processing is intrinsic to the perception of shape, important questions remain about the nature of this interaction. For example, we cannot infer whether the interference observed in the behavioral work includes cross-stream interactions or results solely from operation within the dorsal visual stream. As reviewed above, there is evidence that object shape is represented in the dorsal stream (e.g., Konen & Kastner, 2008), raising the possibility that dorsal stream processing of shape could potentially occur independently of ventral shape perception. Functional and anatomical connectivity between ventral and dorsal stream regions that are active during shape change detections might be explored as a marker for possible perceptual interactions between the two visual pathways.

Role of Attention

Attention-related activity in frontal and parietal areas is often associated with attentional, capacity-demanding operations (Kastner & Ungerleider, 2000). As such, there might be concern that the activation patterns observed in the above experiments originate from attentional processes rather than processes associated with shape or location perception. It is indeed very difficult to account for all the mitigating factors, which may contribute to distinct functional activation in the ventral and dorsal areas of the visual system. Several precautions, however, have been implemented to the design of our experiments to minimize the effect of attention on our findings as much as possible. Both tasks utilize the same stimuli at the same on-screen locations. Both tasks have been matched in terms of behavioral performance, and eye tracking data indicate that participants were fixating at the same on-screen locations in both tasks. Furthermore, activity within posterior parietal cortex in response to the increase in difficulty did not differ between the two tasks. On the basis of the above factors, we assume that most, if not all, of the activity related to the focus and shifts of attention has been subtracted out from the RFX contrast comparisons. To that end, it becomes very unlikely that an imbalance of attentional demands is the driving force behind the activation patterns we observed.

A second concern would be that, although the attentional demands might be balanced across the two tasks, the distribution of spatial attention on the visual stimuli might still differ. For example, the horizontal line, which was part of both tasks, was clearly more important for the location task and less important for the shape task. This difference in allocation of attention between the object and line could result in differential activation patterns between the two tasks across the ventral and dorsal visual streams. This scenario, however, is also unlikely. The magnitude of activation in posterior parietal cortex in response to the shape task was equal to the magnitude of activation during the location task. Assuming that posterior parietal cortex is an attentional marker, the findings cannot simply be the result of attentional modulation.

Limitations of the Pattern of Eye Fixations Analysis

The effective resolution of the eye tracker, after adjusting for head motion/drifts and the spatial jittering of the objects on the screen, was about 2° of visual angle which is similar to the on-screen size of the individual object images. As such, there is a concern that, although we report comparable numbers of eye fixations across tasks, it might still be the case that, within the defined AOIs (within each object), differences between the conditions are still present. We think this is unlikely for several reasons: (1) There is a relatively small number of fixations per trial (on average four fixations per trial for all conditions, across two objects on a screen). Examination of the scan paths indicates that participants were looking at each object twice, on average, before issuing a response and it is unlikely that this pattern will change even if we were to acquire data at a higher eye-tracking resolution. (2) Subdividing the initial AOIs is not straightforward. For example, informative sub-AOIs would have been the top/bottom parts of objects or the left/right parts of objects. Because of the large number of objects used, however, up/down as well as left/right is not defined similarly for all objects (e.g., from Figure 2D, the top part of the frying pan image is not at the same location as the top part of the house image). For this reason, labels such as top/bottom or left/right become relatively meaningless when we average across objects. Alternatively, we could have used AOIs defined individually per object, but again because of the large number of objects used it would not have been surprising if we found no statistical differences between conditions because of the small number of samples per object. More detailed exploration of the eye movements in tasks such as those used here might be useful but, as we tentatively suggest, we expect the findings to remain unchanged.

Future Directions

As summarized above, the findings from the fMRI and behavioral studies suggest that spatial location processing mechanisms that operate at the level of the scene, presumably within the dorsal visual pathway, can contribute to shape processing. However, the precise nature of the dorsal stream contribution to shape perception is not yet clear and needs to be explored further. One hypothesis is that the contribution of the dorsal visual stream to shape perception is similar to that of the ventral visual stream but is perhaps weaker or less robust, making it more difficult to uncover. Alternatively, the two streams might contribute to shape perception differently.

If the latter alternative is true, one hypothesis is that the common resource used in scene-based location processing and in detecting shape differences between objects arises because changes in an object's shape alter locations as well, but with respect to the object and the elements that constitute that object rather than to the scene. By such an account, the analysis of location is intrinsic to the processing of shape, and mechanisms devoted to object locations in scenes can be recruited for the requisite processing of locations in objects. The connection between shape and location within objects is supported by theories proposing that objects are perceived as a conjunction of shape features, marked by points of concavity on local contours and bound to specific relative locations (Op de Beeck, Torfs, & Wagemans, 2008; Hayworth & Biederman, 2006; Biederman, 1987). Under this framework, some aspect of location processing is integral to the perception of shape.

Under the above scenario, however, another hypothesis might also be valid. It might be the case that the withinobject, location process described above is separate and independent from the set of shape processes associated with the ventral visual pathway and the processing of shape differences between objects. If so, it remains possible that the dorsal visual pathway may not contribute to shape processing per se but may activate exclusively in response to a separate and independent visuospatial component that operates at the level of the object's structure.

Many questions remain, and indeed many more have been generated as a result of the current findings. What is key is that the binary distinction between the two cortical pathways no longer seems tenable and that future investigations designed to explore the representational and computational mechanisms mediated by each pathway are urgently needed.

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Notes

1. The results based on RT and Accuracy reveal very similar findings to each other (and to the inverse efficiency results). There is no significant interaction between Task type and Difficulty level (p = .08 for Accuracy, p = .21 for RT). The p value for Accuracy, however, is marginally close to significance so we went ahead and run pairwise comparisons for all conditions, separately for RT and Accuracy. According to the pairwise comparisons, RTs are very closely matched (smallest p = .33; 1090 msec for easy location vs .1037 msec for easy shape). Accuracy approached marginal significance (p = .074; 88% for difficult shape vs. 93% for difficult location). Given this result, even though RTs are closely matched, participants are tending to be slightly less accurate for difficult shape compared with difficult location. This small accuracy difference may potentially imply a speed–accuracy tradeoff (participants might

have sacrificed some accuracy for difficult shape to gain some speed). It is partly for this reason that we adopted inverse efficiency as the dependent measure (it essentially weights the RT based on accuracy) and will account for speed–accuracy tradeoffs if present. However, we did not find any differences between shape and location change detections across difficulty levels (easy shape vs. easy location and difficult shape vs. difficult location) using this method.

2. Note that in the ROI analyses above we are sometimes comparing activation levels across anatomically separate brain regions (IPS vs. LOC). Between-ROI activity comparisons are usually problematic for a number of reasons, such as signal-tonoise ratio differences and magnetic field inhomogeneities. We are performing these comparisons based solely on the finding that the primary activity (shape change activity for LOC, location change activity for IPS) is matched across both peak-centered and midpoint ROIs (shape change activity in LOC is comparable with location change activity in IPS). Given this matching in primary activity, the question we are asking is whether the nonprimary activation within these ROIs will also match and whether the magnitude of this nonprimary activity will be comparable to the magnitude of the primary activity.

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