A Stimulus-Driven Approach to Object Identity and Location Processing in the Human Brain

René Marois,*‡ Hoi-Chung Leung,†
and John C. Gore†
*Department of Psychology
Vanderbilt University
Nashville, Tennessee 37240
†Department of Diagnostic Radiology
Yale University School of Medicine
New Haven, Connecticut 06511

Summary

The primate visual system is considered to be segregated into ventral and dorsal streams specialized for processing object identity and location, respectively. We reexamined the dorsal/ventral model using a stimulus-driven approach to object identity and location processing. While looking at repeated presentations of a standard object at a standard location, subjects monitored for any infrequent "oddball" changes in object identity, location, or identity and location (conjunction). While the identity and location oddballs preferentially activated ventral and dorsal brain regions respectively, each oddball type activated both pathways. Furthermore, all oddball types recruited the lateral temporal cortex and the temporo-parietal junction. These findings suggest that a strict dorsal/ventral dual-stream model does not fully account for the perception of novel objects in space.

Introduction

Perceiving the location and identity of objects in the environment is among the most basic functions of the primate visual system. Given their importance, it is not surprising that so much neural computation appears devoted to these functions (Felleman and Van Essen, 1991). More surprising are the early findings, first derived from primate neurophysiology and supported by human neurofunctional studies, that the neural substrates mediating object and location processing appear functionally segregated into two major anatomically distinct pathways (Ungerleider and Mishkin, 1982; Haxby et al., 1991, 1994; Kohler et al., 1995; Clark et al., 1996; Courtney et al., 1996; Belger et al., 1998). Object identity, including its shape, color, and associated semantic features, appears to be encoded in the inferior occipital and temporal lobes of the visual system, while object location is processed by the parietal and superior occipital lobes of the visual system.

While the predominant role of the ventral pathway in object identity processing has been largely confirmed, the function of the dorsal pathway is still debated. First, neuroimaging studies have demonstrated the involvement of the parietal cortex, especially the superior parietal and intra-parietal areas, in visuo-spatial attention

‡ To whom correspondence should be addressed (e-mail: rene. marois@vanderbilt.edu).

rather than simply for spatial perception (Corbetta et al., 1993, 1998; Nobre et al., 1997; Vandenberghe et al., 1997; Coull and Nobre, 1998; Kastner et al., 1999). Second, both human brain lesion and primate neurophysiological studies indicate that the dorsal stream may be involved in the intention to generate movements as well as in the visual transformations they require (Goodale and Milner, 1992; Milner and Goodale, 1995; Andersen et al., 1997). Consistent with this possibility, superior/intra-parietal areas are engaged with eye movements (e.g., Anderson et al., 1994; Corbetta et al., 1998; Luna et al., 1998). Third, it has recently been argued that tasks that do not explicitly manipulate spatial attention can also activate similar parietal cortex regions (Coull and Nobre, 1998; Le et al., 1998; Wojciulik and Kanwisher, 1999). Taken together, these results suggest that the intra-parietal and superior parietal cortex may be involved in the general maintenance, distribution, and control of attention and action rather than in spatial attention per se.

The unresolved debate regarding the dorsal stream's function may be partly attributed to the limited scope of experimental paradigms that have been used to study this issue. In particular, virtually all functional neuroimaging studies comparing the roles of the dorsal and ventral streams have used a task-driven approach (e.g., Haxby et al., 1991, 1994; Kohler et al., 1995; Clark et al., 1996; Courtney et al., 1996). In such paradigms, the subject's attention periodically alternates between the location and identity of objects in the display while stimulus presentation is constant throughout the task. Any activated region can therefore be identified as subserving either spatial or object identity processing. Although task-driven paradigms have helped reveal the relative functions of the ventral and dorsal pathways for top-down control of attention, they may not provide a complete picture of the interaction between visual attention and perception. For instance, the results obtained in a task-driven paradigm depend on whether an attentional manipulation can selectively bias and drive *all* of the neural substrates mediating object identity and location processing. Although implicit, this assumption has never been formally investigated. An additional limit of the task-driven approach is that spatial perception is involved in both (identity and location) conditions since objects are constantly shown at different positions. Thus, the standard object location/identity paradigm investigates the control of visuo-spatial attention but not spatial perception per se, as the activation related to perceiving a change in the environment would cancel out when directly comparing the two conditions. Finally, although a direct comparison of object identity and location processing is a powerful approach to reveal differences between conditions, it has the drawback of potentially concealing areas that are involved in processing both attributes.

We have reexamined the dorsal/ventral model of object location and identity processing with an experimental design that is the "bottom-up" counterpart to the task-driven approach. In this stimulus-driven approach
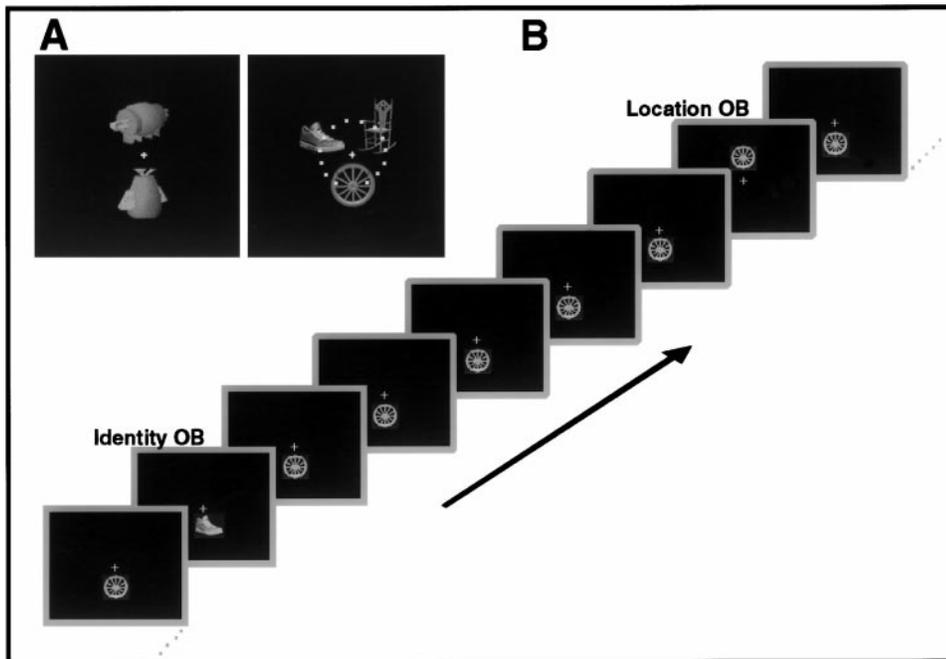
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Figure 1. Experimental Protocol

(A) The stimuli consisted of either unfamiliar (left inset, experiment 1) or familiar objects (right inset, experiments 1 and 2). The position of the possible object locations is indicated in the right inset by a circular array of 14 dots (not visible in experiment), with the wheel positioned below the fixation point serving as the standard in this example. Two other objects are shown as stimulus examples in right inset.

(B) Trial design. The display consisted of black frames with a central fixation cross that subjects were instructed to attend at all times. Every 1650 ms an object was presented for 180 ms. For 86% of the trials, the object was the standard stimulus at the standard position, with the rest of the trials consisting of another object shown at the standard position (identity oddball), the standard object at a different position (location oddball), or a different object at a different location (conjunction oddball, not shown). Subjects' task consisted in indicating the presence of the standard object at the standard location by pressing one button and the presence of *any* type of oddballs by pressing another button.

(Figure 1), a standard object is briefly and repeatedly presented at a standard location. Infrequently, a novel object is substituted at the standard location (object oddball), or the standard object is presented at a novel location (location oddball), or a novel object is presented at a novel location (conjunction oddball). Since the subject's task is simply to indicate by button-press the presence of any of the three oddballs, his/her attention is not biased toward a specific attribute. Stimuli that markedly differ in spatial or featural characteristics from the rest of a visual scene are salient to our visual system and generally lead to attentional capture (Egeth and Yantis, 1997). Thus, activation associated with each oddball should be related to the perception of a particular feature's novelty and orienting of attention to the stimulus. Our approach represents an extension of a priming or adaptation paradigm (Miller et al., 1991; Buckner et al., 1998; Grill-Spector et al., 1999). In this technique, the neuronal response is habituated (decreased) with the repeated presentation of a standard stimulus (e.g., Miller et al., 1991; Buckner et al., 1998). The oddballs for a given feature lead to an enhanced response in the brain areas that encode changes in this dimension. Applied to the present study, this paradigm should reveal brain regions responsible for detection and discrimination of changes in object identity and/or location. The activation differences between the oddball types can therefore inform us about the differential processing of object

identity and location in the absence of top-down attentional biases.

Results

Experiment 1, Single Oddballs

A correlation analysis was used to reveal the activation pattern associated with each of the three types of oddballs. The identity oddballs activated both ventral and dorsal cortical areas (Figure 2A). Posteriorly, the activation was localized to extrastriate regions of lateral occipital cortex, and anteriorly, the activation followed two main routes: a ventral path along the temporal cortex and a dorsal path along the intra-parietal cortex ("route" or "stream" is used here to describe activation patterns that extend from "early" visual areas into more anterior and associative areas; our results do not allow us to infer the unfolding of the activation patterns in time). The activation associated with the location oddballs showed both similarities and departures from the object identity–related activation. Similar to the identity oddballs, the location condition engaged lateral occipital cortex and anterior ventral temporal cortex (Figure 2B). In addition, the location oddballs recruited at least one or more areas in occipital cortex dorsal to the lateral occipital cortex activation. The dorsal activation proceeded anteriorly into the posterior parietal and intra-parietal cortex. In addition to these regions, a series of lateral areas,
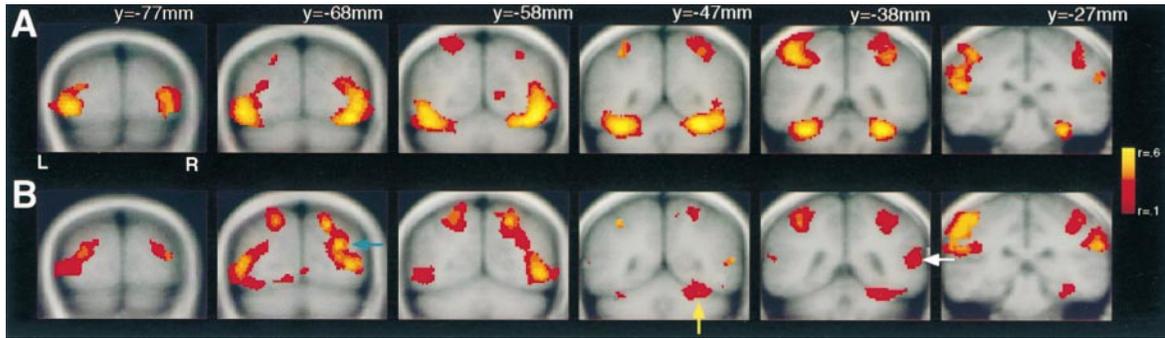
Figure 2. Group Composites of Experiment 1

(A) Activation results for the identity oddballs. Activation was predominantly found in lateral occipital cortex posteriorly and in parietal and temporal cortex anteriorly. The y Talairach coordinates are indicated at the top of each frame. Abbreviations: L, left hemisphere; R, right hemisphere.

(B) Activation results for the location oddballs. Activation was found in lateral and dorsal occipital cortex and in parietal cortex. The green arrow indicates an activation site in superior occipital cortex, the yellow arrow indicates inferior temporal cortex activation, and the white arrow indicates activation at the temporo-parietal junction (TPJ).

particularly in the middle temporal gyrus and at the junction of the temporo-parietal cortex, were also recruited by the location oddballs (Figure 2B). The anatomical localization of the activated areas was also confirmed by examination of single subjects' data.

Conjunction Oddballs

A clearer picture of the different streams of activation can be observed with the conjunction oddballs (Figure 3). From the lateral occipital cortex activation, there seems to be not two but three major parallel pathways as one proceeds from the occipital areas toward anterior brain regions. Dorsally, the activation runs from the superior occipital sulcus into the parietal cortex to course along the intra-parietal sulcus. Ventrally, the activation follows the inferior temporal gyrus and the collateral sulcus. In addition, a third lateral stream can be discerned between the two others: from the lateral occipital area, activation occurs along the middle temporal cortex and proceeds anteriorly along the superior temporal sulcus up to the temporo-parietal junction (TPJ) and inferior parietal lobule.

The activation associated with the conjunction condition encompassed the areas activated by both the identity and location oddballs. In fact, the group composites for the conjunction oddballs did not reveal any novel area not engaged by one or the other of the two single oddballs.

Location Versus Identity

The results of the single oddball analyses revealed a distributed pattern of activation, with each oddball activating both dorsal and ventral pathways. These results contrast with prior PET and fMRI task-driven experiments that supported a dorsal/ventral functional dissociation of identity and location processing (e.g., Haxby et al., 1991, 1994; Kohler et al., 1995; Clark et al., 1996; Courtney et al., 1996). However, these studies directly compared the activation in location and identity conditions. We therefore assessed whether a similar dorsal/ventral pattern would be found with the stimulus-driven approach using a similar direct comparison. Very few sites survived direct comparison, suggesting that using a stimulus-driven paradigm, location and identity processing have more in common than when attention is biased toward each dimension (Figure 4). Nevertheless, and consistent with the classical top-down framework, the lateral occipital and inferior temporal cortex were more activated with the identity oddballs. Moreover, the only activation selectively associated with the location oddballs occurred in the superior occipital and parietal cortex, in sites that were identified with the single oddball analysis (compare with Figure 2B). These results have three important implications. First, the sparseness of oddball-specific activation supports our initial findings of a significant overlap in the neural networks activated by each condition. Second, the activation that did
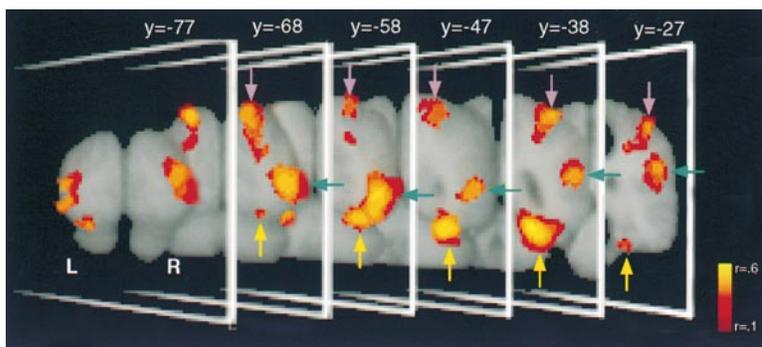

Figure 3. Group Composites of Conjunction Oddballs for Experiment 1

Oblique perspective with the white frame denoting each slice plane. From the lateral occipital cortex posteriorly, the activation continues anteriorly in three major directions: dorsally in the superior parietal and intra-parietal cortex (purple arrows); ventrally in the temporal cortex (yellow arrows); and laterally in the middle/superior temporal and temporo-parietal cortex (green arrows).
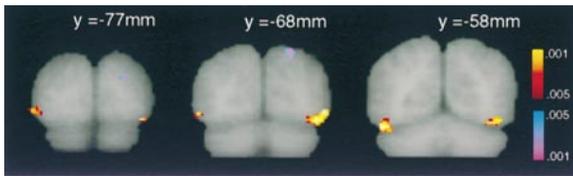
Figure 4. Group Composites of the Contrast Analysis between Identity and Location Oddballs

Areas that activated more in the identity oddballs were located in lateral occipital and inferior temporal cortex (yellow), while those which activated more with the location oddballs were in the superior occipital and posterior parietal cortex (blue). No other regions were activated in the brain.

survive the analysis is in agreement with the task-driven findings. This suggests that task-driven attention may influence the response of overlapping neural networks for object location and identity processing, enhancing biases already present in stimulus-driven perception. Third, the absence of lateral cortex activation in the location versus identity comparison supports the notion that this region is activated in each single oddball condition.

Experiment 2, Replication

We replicated the first experiment with some minor alterations. First, only familiar objects were used as stimuli. Second, all three types of oddballs (instead of any given two) were included in every run. Third, in addition to using the pixel-based approach described in experiment 1, we performed a region of interest (ROI) analysis based on the brain regions activated in the first experiment to determine the replicability of our initial findings. The pixel-based approach and the ROI analysis confirmed the results of the first experiment (Figure 5; Table 1):

each oddball type significantly activated nearly all ROIs. As exceptions, the location oddballs did not significantly activate the lateral occipital and anterior fusiform cortex, while both the identity and conjunction oddballs failed to recruit the medial part of the superior parietal cortex (precuneus). These exceptions aside, the ROIs were significantly activated by each of the three oddball types, confirming the presence of a distributed network associated with each oddball type.

The ROI analysis also revealed significant activation in the lateral areas (namely the middle temporal, temporo-parietal, and inferior parietal areas) for the identity oddballs. This identity-related activation is also evident in the composite maps (Figure 5). To determine whether the identity condition also activated this pathway in the first experiment, albeit below the statistical threshold applied to the group composites, we applied the ROI of the lateral strip activated by the location and conjunction oddballs to the identity condition in the first experiment. This analysis confirmed that the identity oddballs also recruited the lateral strip of activation even in the first experiment (for TPJ ROI, mean $r = 0.14$, $t = 5.048$, $p < 0.0001$; for middle/superior temporal ROI, mean $r = 0.16$, $t = 6.76$, $p < 0.0001$). We could not determine with consistency, either from examination of the group composites or single subject data, the number of distinct areas contained in the lateral strip of activation.

The activation observed in dorsal cortex with identity oddballs and in ventral cortex with location oddballs is not simply due to the contamination of the hemodynamic response to one oddball by the trailing or leading edges of the response to different, temporally adjacent oddballs. If contamination occurred, comparison of the activation at the estimated peak of the response (3.3–6.6
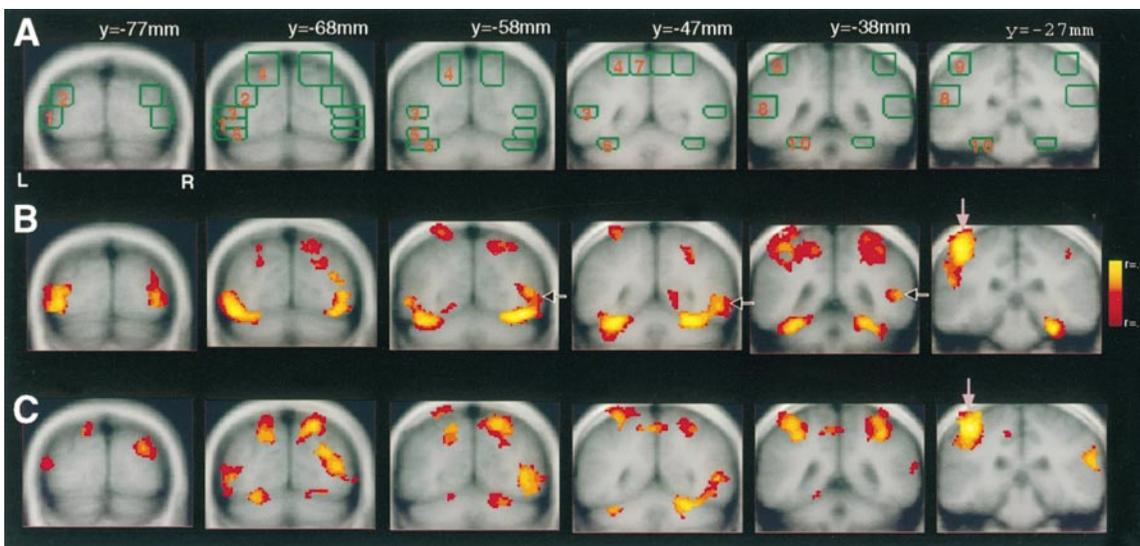

Figure 5. Group Composites of Experiment 2

(A) ROI partitioning based on activated regions in experiment 1. ROIs: (1) lateral occipital cortex, (2) superior occipital cortex, (3) middle/superior temporal cortex, (4) superior parietal cortex, (5) inferior temporal gyrus, (6) posterior fusiform, (7) precuneus, (8) TPJ/inferior parietal cortex, (9) intra-parietal sulcus, (10) anterior fusiform/parahippocampal gyrus.
(B) Activation results for the identity oddballs. In addition to the lateral occipital, inferior temporal, and intra-parietal activation, activation in lateral temporo-parietal cortex is also visible (black and white arrow).
(C) Activation results for the location oddballs. Note the left anterior parietal activation in both oddball types (purple arrow).

Table 1. ROI Analysis of Experiment 2

ROI		Talairach Coordinates			Mean r Values		
		x	y	z	Identity	Location	Conjunction
(1)	r	42	−77	6	0.22	0.13*	0.26
	l	−43	−77	6			
(2)	r	33	−76	26	0.13	0.17	0.23
	l	−33	−76	26			
(3)	r	45	−62	13	0.15	0.16	0.16
	l	−46	−63	13			
(4)	r	20	−62	50	0.13	0.21	0.17
	l	−21	−63	51			
(5)	r	42	−66	−5	0.27	0.17	0.26
	l	−43	−66	−5			
(6)	r	35	−55	−15	0.30	0.15	0.29
	l	−35	−55	−15			
(7)	r	8	−48	54	0.01*	0.17	0.08*
	l	−8	−48	54			
(8)	r	53	−34	21	0.15	0.15	0.11
	l	−54	−34	23			
(9)	r	41	−35	52	0.22	0.22	0.23
	l	−41	−34	53			
(10)	r	25	−34	−16	0.23	0.05*	0.18
	l	−27	−35	−16			

Coordinates represent the center of mass of activation in each ROI. The mean r values are all significant ($p < 0.05$, with Bonferroni correction) except for those marked with an asterisk. ROI definitions are based on experiment 1. ROIs: (1) lateral occipital cortex, (2) superior occipital cortex, (3) middle/superior temporal cortex, (4) superior parietal cortex, (5) inferior temporal gyrus, (6) posterior fusiform, (7) precuneus, (8) TPJ/inferior parietal cortex, (9) intra-parietal sulcus, (10) anterior fusiform/parahippocampal gyrus. Abbreviations: r, right hemisphere; l, left hemisphere.

s after stimulus presentation) with the activation associated with the rising/falling phases of the response should yield a very different pattern of activation to that observed with the correlational analysis since any contamination would be more associated with the edges than with the peak of the response. Contrary to this prediction, comparison of the mean signal intensity at the peak and edges of the response revealed a very similar pattern of activation to that obtained with the correlational analysis for both the identity and location oddballs (cf. Figure 5 with Figure 6). Cross-pathway activation was even observed under conditions where contamination cannot occur: ventral (temporal cortex) activation could be discerned in four subjects who were shown only location oddballs (Figure 7). Even with this limited sample size of four subjects, an ROI analysis, using the anterior fusiform ROI defined in experiment 2, demonstrated marginally significant activation ($p = 0.06$) with location oddballs. Taken together, these findings indicate that interoddball hemodynamic contamination cannot account for the present results.

Experiment 3, Visual Motion Control
In addition to the ventral and dorsal pathways typical of task-driven studies, a lateral strip of activation was identified in experiments 1 and 2, encompassing the lateral temporal, occipital, and parietal cortex, regions that typically include motion-selective areas (Tootell et al., 1995; Van Oostende et al., 1997). We considered the possibility that this activation could be explained by motion perception. Illusory motion of the object between the standard and oddball positions is very unlikely to cause the present activation because the interstimulus interval (1470 ms) is too long to trigger such an illusion (Anstis, 1986). However, motion-sensitive areas can also respond to imaginary or implied motion (Kourtzi and Kanwisher, 2000). Although implied motion may account for some of the activation associated with the location oddballs (when the same object appears in a new location), it is more difficult to understand how implied motion could account for the activation observed with the conjunction oddballs and especially the identity oddballs. Despite these caveats, an additional experiment was performed to determine whether the lateral activation could still be obtained under conditions unlikely to yield implied motion. In this experiment, subjects monitored the number of instances of a particular letter shown at fixation among a rapid serial visual presentation of distractor letters. Every 12 s, a simple but salient
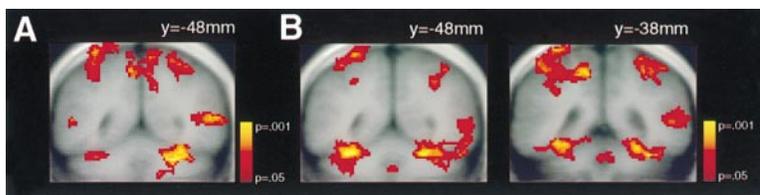

Figure 6. Selectivity of Oddball Activations

(A and B) Statistical parametric maps of the mean signal intensity for the peak compared to the flanks of the hemodynamic response for experiment 2. Location (A) and identity (B) oddballs each significantly recruited the same parietal, temporal, and temporo-parietal areas observed with the correlational analysis (cf. Figure 5). Statistical parametric maps are thresholded at $p < 0.05$.
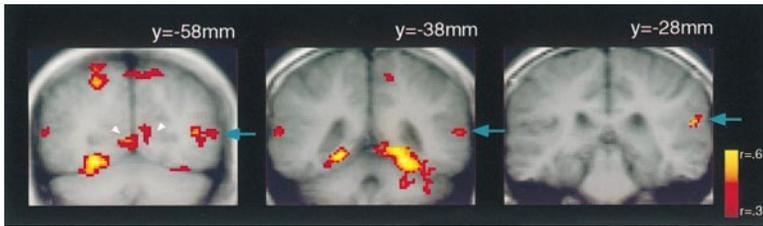
Figure 7. Group Composites of Experiment 3

The lateral temporal and temporo-parietal activation (green arrow) with peripheral object presentation was observed even when the subjects performed a highly demanding central task. Note the inferior temporal and superior occipital/parietal activation, as well as putative anterior V1 activation (white arrowheads).

object (wheel) was briefly presented in one of four peripheral positions (above, below, left, and right of fixation). The peripheral object was irrelevant to the monitoring task. If implied or imaginary motion accounts for the lateral activation in previous experiments, it is unlikely to occur in this case because of the long delay (12 s) between peripheral object presentations and because attention is focused on a highly demanding central task. The mean accuracy in the monitoring task was 72% during the fMRI experiment, confirming the subjects' reports of the task's considerable difficulty. Nevertheless, the correlational analysis shows clear activation associated with peripheral object presentation along the lateral temporo-parietal cortex (Figure 7). This finding was corroborated by an ROI analysis of the middle temporal and temporo-parietal areas as defined in experiment 2. The middle temporal and TPJ ROIs were both significantly activated (mean $r = 0.21$, $p < 0.01$; mean $r = 0.18$, $p < 0.05$, respectively).

Experiment 1 Revisited, Motor Control

In a final analysis, we directly addressed the role of the motor response in the lateral and superior parietal activation. Although all stimulus presentations required a motor response, the response mapping was different for the oddball and standard presentations. This response remapping is likely to be reflected in the activation patterns, in particular in the anterior parietal cortex where preliminary observations in experiment 1 denoted a stronger activation in the left hemisphere for all oddballs. It is reasonable to expect the left hemisphere to be associated with the motor response as the right-handed subjects used their dominant hands for the task. To test whether this or any other parietal activation was related to motor response mapping, 9 of the 20 right-handed subjects in experiment 1 used their nondominant (left) hands for responding. Using a contrast analysis, we compared the activation between the groups who used their dominant (right) versus nondominant (left) hand. The results demonstrate a left-hemisphere activation in the parietal cortex with use of right hand (Figure 8), consistent with recent findings of greater asymmetric activation when right-handed subjects use their dominant compared to their nondominant hands (Singh et al., 1998). The Talairach coordinates of this activation place it in the postcentral gyrus ($x = -30$, $y = -29$, $z = 60$). Importantly, the inferior parietal/temporo-parietal junction activation was not affected by the hand manipulation.

Discussion

The results indicate that stimulus-driven attention to the dimensions of object identity and location bears similarities with as well as distinctions from the neural networks associated with a top-down attention to these dimensions.

The most obvious similarities of stimulus-driven attention to the classical what/where picture offered by the task-driven approach pertain to the dorsal/ventral pattern of activation. The identity oddballs activated the lateral occipital cortex as well as the ventral temporal (fusiform). These two regions are often noted as responsive to various aspects of object shape and identity processing (Malach et al., 1995; Ungerleider, 1995; Kanwisher et al., 1997; Grill-Spector et al., 1998, 1999; Ishai et al., 1999; reviewed by Treisman and Kanwisher, 1998). Reciprocally, presentation of location oddballs elicited responses in cortical regions that are known to be involved in visuo-spatial attention tasks, i.e., superior occipital and parietal cortex (Haxby et al., 1991, 1994; Corbetta et al., 1993, 1998; Kohler et al., 1995; Nobre et al., 1997; Vandenberghe et al., 1997; Coull and Nobre, 1998; Kastner et al., 1999). This dorsal/ventral distinction in stimulus-driven object location and identity processing is supported by a direct comparison of location with identity oddballs, showing location-related activation in the superior occipital and parietal cortex and identity-related activation in the lateral occipital and inferior temporal cortex.

The dorsal/ventral distinction for object location and identity processing is only relative, however, as each oddball type was found to activate *both* of the pathways. We conclude that the dorsal and ventral pathways are both engaged by any novel object in space and that the what/where distinction originally demonstrated under task-driven conditions is not as sharp under stimulus-driven conditions. A strong confirmation of this hypothe-
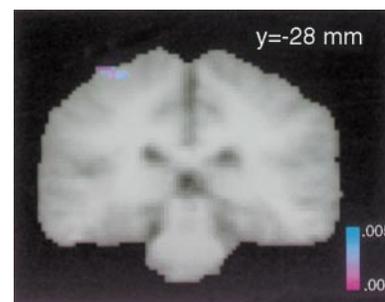

Figure 8. Group Composites of the Right Versus Left Hand Use in Motor Response

A single left parietal cortex area in the postcentral gyrus ($x = -30$, $y = -29$, $z = 60$) was more activated when right-handed subjects used their right hand than when they used their left hands to respond.

sis will await a direct comparison of task-driven and stimulus-driven processing within the same experiment.

The role that the cross-pathway activation may play is presently unknown. It is possible that the parietal recruitment with the object-identity oddball occurs indirectly via the activation of the ventral pathway instead of directly through early visual centers. This is supported by the existence of anatomical connections linking the dorsal and ventral pathways (Goldman-Rakic, 1988; Felleman and Van Essen, 1991; Distler et al., 1993). Alternatively, the dorsal activation with the object identity–related oddball may be related to the capture, rereorienting, or enhancement of attention to any novel stimulus presentation. For instance, the presentation of a novel object feature may elicit a general increase in attention to all the dimensions of the (novel) object, suggestive of an object-based attention process (Duncan, 1984, 1993; O'Craven et al., 1999). The parietal cortex activation associated with identity oddballs may also reveal a role of the dorsal pathway in object identification. Neurophysiological studies in macaques have shown that parietal neurons can also encode object shape (Taira et al., 1990; Sereno and Maunsell, 1998). These findings are consistent with brain lesion studies demonstrating that dorsal parietal areas are involved in normal object perception (Robertson et al., 1997). While the functional contribution of the dorsal parietal cortex in object identification remains to be precisely determined, its involvement may also depend on the task at hand. For instance, the parietal cortex may be more engaged in object processing when subjects make spatial relation judgements about an object (Aguirre and D'Esposito, 1997; Fink et al., 1997).

Some of the temporal cortex activation with location oddballs may be attributable to the retinotopic representations of space in early visual areas extending in temporal cortex (Tootell et al., 1996). Additionally, while the ROI analysis failed to demonstrate significant activation in anterior fusiform in experiment 2, the pixel-based approach of experiments 2 and 3 as well as the ROI analysis of experiment 3 suggest that location oddballs do engage this brain region. The discrepancy may be due to the imperfect fit between the region of interest and the location of the activation: this activation appears to be localized to the parahippocampal gyrus (PHG; see Figure 7). Interestingly, this area has been implicated in various aspects of topographical information processing (Aguirre et al., 1996, 1998; Aguirre and D'Esposito, 1997; Epstein and Kanwisher, 1998; Epstein et al., 1999). The Talairach coordinates of the present activation corresponds strikingly to the location of the "parahippocampal place area" (PPA; x, y, z: 22, −38, −6 compared to 20R and 28L, −39, −5 for the PPA; Epstein and Kanwisher, 1998). It is therefore tempting to speculate that the PHG is activated in the present task because of the novel encoding of the spatial layout with each location oddball presentation. However, the identity oddballs also appear to recruit a similar region (Figures 2A, 5B, and 6B). Given that temporal cortex areas near the PHG respond to object presentations (e.g., Ishai et al., 1999), it is difficult to conclude at this point whether the location and identity oddball activated identical or adjacent neural substrates. Regardless of the relative spatial extent of activation associated with each oddball

type, the present findings demonstrate that the PHG can be activated even when attention is summoned to another cognitive function and the stimulus is merely an irrelevant distractor (see Figure 7). This strongly suggests that the PHG may be activated automatically by novel visual stimuli (Epstein and Kanwisher, 1998). Taken together, the inferior temporal/parahippocampal activation with object location oddballs demonstrate that at least some aspects of the spatial information in the visual scene may be encoded in the ventral stream (Aguirre and D'Esposito, 1997; Epstein and Kanwisher, 1998; Epstein et al., 1999), while the parietal activation with identification oddballs indicate the involvement of the dorsal attention systems in nonspatial information processing, negating a strict dorsal/ventral dissociation between object location and identity processing. However, not all ventral areas responded to the spatial condition. Notably, the lateral occipital and adjacent inferior temporal cortex were not significantly modulated by the location oddballs. Its location suggests that it corresponds to LO (PF/Loa), an object-responsive area that exhibits position-invariant activation (Malach et al., 1995; Grill-Spector et al., 1999).

Feature Conjunction Processing

As predicted from the response to the single-dimension oddballs, the conjunction oddballs recruited both the dorsal and ventral pathways as well as areas of the lateral temporo-parietal cortex. No brain regions were specifically activated by the conjunction stimuli, suggesting that the location and identity of a novel stimulus are encoded by a distributed network of temporal, occipital, and parietal visual areas. How visual features that belong to the same object are "bound" together into a single coherent unit is a matter of intense debate (see Roskies, 1999 and references therein). One attractive theory is that one or a few specific brain regions involved in spatial attention orchestrate the conjunction of visual features (Treisman and Gelade, 1980; Treisman, 1993). Another group of theories suggests that visual feature conjunction occurs through direct interaction between different visual areas via some form of temporal binding of their activity pattern (reviewed by Gray, 1999). Our finding of significant cross-pathway activation with each oddball type also provides another mechanism by which binding may occur since there may be multiple ventral and dorsal sites that carry both types of information. This possibility is supported by neurophysiological experiments demonstrating that cells in the parietal cortex, traditionally regarded as spatial information processors, can encode shape (Taira et al., 1990; Sereno and Maunsell, 1998). However, our results cannot discount the possibility that specific areas involved in visual feature binding went undetected with the present experimental paradigm. For instance, the neural mechanisms underlying visual feature binding may be reset with *any* oddball presentations (the perception of a novel object at a standard location would still need the binding of these two features to be experienced) or even with *every* stimulus presentations. Conjunction areas would be less discernable if they showed little or no repetition response suppression.

Temporo-Parietal Activation

In addition to the dorsal and ventral pathways, all three oddball conditions recruited lateral cortical areas, spanning the lateral occipital, middle, and superior temporal cortex, and the junction of the temporal and parietal cortex, including the inferior parietal lobule.

The posterior section of this activation strip in lateral temporal cortex may overlap with regions specialized for motion processing (MT+; DeYoe et al., 1996), as suggested by the corresponding Talairach coordinates (Table 1; Tootell et al., 1995; Van Oostende et al., 1997). The MT+ complex is known to respond to abrupt visual onsets and offsets and appears to contain a topographic representation, albeit gross and distorted, of the visual field (Van Essen et al., 1981; Maunsell and Van Essen, 1983a; but see Tootell et al., 1995, 1998). Given that MT+ has a predominant parafoveal/peripheral representation of visual space (DeYoe et al., 1996) and that our stimuli were presented parafoveally, it is not surprising that MT+ would be activated by the abrupt presentation of a stimulus at a novel location. While it is harder to account for the activation of similar or surrounding areas with object identity oddballs, any gross shape differences between the oddballs and the standard may lead to activation of cells whose receptive fields were not activated by the repetitive presentation of the standard object. The possibility that the middle temporal area encodes gross shape differences is supported by the finding that neurons of macaque MT are selective to the orientation of stationary, flashed bars (Maunsell and Van Essen, 1983b). A better understanding of the role of motion-sensitive areas in stimulus-driven object identity and location processing will require functional mapping of MT+ in the same subjects.

The anterior portion of the lateral activation is localized to the TPJ and inferior parietal lobule. These areas appear to respond to the presentation of visual (this study; McCarthy et al., 1997) and auditory oddballs (Menon et al., 1997; Opitz et al., 1999). Although the TPJ has not been well characterized functionally, lesions in this region often lead to the syndrome of neglect in humans (Vallar and Perani, 1986). Patients suffering from neglect typically fail to explore and explicitly perceive visual, auditory, and/or somatosensory stimuli located in the contra-lesional space (Robertson and Marshall, 1993). Neglect is thought to reflect a failure of the attentional system to bring stimuli into awareness (Driver and Mattingley, 1998). The present results are consistent with this hypothesis since this area is activated in the presence of novel stimuli. Furthermore, oddballs elicit in healthy individuals a characteristic electrophysiological response (P300) that is affected in neglect patients with TPJ lesions (Lhermitte et al., 1985; Verleger et al., 1994; Knight, 1997). Recent evidence that neglect can be object based as well as space based (e.g., Humphreys et al., 1994; Behrmann, 2000; Robertson and Rafal, 2000) is also entirely consistent with the present results since both object location and identity oddballs activated the same temporo-parietal area. Taken together, these findings are consistent with the idea that the TPJ (and inferior parietal lobule) may be involved in the allocation of attention to novel stimuli (reviewed by Rafal, 1996).

The concomitant activation of the posterior lateral temporal cortex and the more anterior TPJ may be more than coincidental. First, Rosen et al. (1999) also observed a stream of activation from the middle/superior temporal cortex to the inferior parietal cortex in their peripheral cueing paradigm, but their study could not discount the possibility that the activation was caused by apparent or implicit motion. Second, there is significant anatomical connectivity between motion-related middle temporal areas and the superior temporal and inferior parietal cortex in the macaque (Boussaoud et al., 1990). It is therefore tempting to speculate that the lateral temporal and parietal areas are functionally connected and that together they play a role in the perception of novel (peripheral) visual stimuli. This notion is supported by the observation that these lateral cortical areas, specifically MT+, respond to stimulus onsets and offsets (Tootell et al., 1995) and that the major input to the middle temporal and parietal areas, the magnocellular pathway (Merigan and Maunsell, 1993), is preferentially activated by the same stimuli that typically produce automatic orientation of attention (Breitmeyer and Ganz, 1976; Yantis and Jonides, 1984; Theeuwes, 1995; but see Yantis and Hillstrom, 1994).

The involvement of the lateral temporo-parietal region in the perception of novel objects in space may help reconcile conflicting views on the functions of the parietal cortex. Specifically, studies of patients with superior parietal lesions showing poor visuo-motor abilities but relatively intact spatial perception (Goodale and Milner, 1992; Milner and Goodale, 1995) are not easily reconcilable with the notion that the parietal cortex is involved in spatial attention. However, both the present neuroimaging data as well as the neuroanatomical evidence in neglect, with brain lesions centering in the temporo-parietal cortex (Vallar and Perani, 1986), suggest that the neural substrates of spatial (and nonspatial) perception of novel stimuli may be dissociated from those of attentional control. We speculate that the intra-/superior parietal cortex may be specially involved in the control of behavior, be it motor (e.g., oculomotor control) or intentional (attentional modulation), while the inferior parietal cortex and temporo-parietal junction may be more involved in the perceptual (stimulus-driven) aspects of attention, such as automatic orienting to novel stimuli (Rafal, 1996).

The present results do not necessarily imply that the middle temporal and temporo-parietal areas can only be activated under stimulus-driven conditions. While there is good evidence for middle temporal activation under task-driven conditions (i.e., when subjects attend to visual motion; Corbetta et al., 1991; Beauchamp et al., 1997; Tootell et al., 1998), the recruitment of the TPJ and inferior parietal cortex in top-down attentional tasks is not evident (Fink et al., 1997). The elucidation of the optimal conditions for driving the latter brain areas, especially the TPJ, will await further investigation.

In conclusion, selective recruitment of the temporo-parietal cortex may represent the most significant difference in the neural mechanisms underlying stimulus-driven and task-driven approach to object identity and location processing. Both approaches activate the classical dorsal and ventral pathways, while the TPJ and surrounding temporo-parietal areas appear to be specifically recruited by the stimulus-driven approach. While it is tempting to think of the latter cortical areas as

forming a singular "lateral" pathway of visual information processing, the usefulness of labeling groups of brain areas as pathways may be very limited as the evidence for parallel distributed processing and plasticity of neural networks accumulates (DeYoe and Van Essen, 1988). Regardless of whether task-driven and stimulus-driven attentional processing is best described as recruiting three (or perhaps even more) distinct visual pathways, it is clear from the present results that a strict model of a dual dorsal/ventral stream of visual information processing is insufficient to account for the perception of novel objects in space.

Experimental Procedures

Subjects
Neurologically normal right-handed subjects were recruited from the Yale University community. Twenty subjects participated in the first experiment (ten female), 14 in the second (four female), and four in the third experiment (two female). All subjects gave informed consent to the protocol that was approved by the Human Investigations Committee of the Yale University Medical School.

Experiment 1
Task Design
The subjects fixated a cross throughout the fMRI runs and pressed one button for every standard stimulus presentation (e.g., wheel below fixation point) and another button for *any* changes (oddballs) from the standard presentation (Figure 1). Oddballs could be a change of object location, identity, or both. Fourteen of the 102 stimuli presented during each run were oddballs. Each run contained two kinds of oddballs (location and identity, location and conjunction, or identity and conjunction). The visual angle between the fixation cross and the center of objects was 1.5°. Objects subtended 2° of visual angle and could clearly be seen from fixation. Each stimulus appeared for 180 ms and the interstimulus interval was 1470 ms. To prevent contamination from verbal/semantic processing (e.g., by naming objects), subjects performed a difficult verbal working memory task concomitantly with the visual oddball task. Each run began with a display of seven consonant letters that subjects constantly rehearsed throughout the run and verbally recalled at the end of each run. Seven to nine runs were collected from each subject. Both the order and timing of oddball presentation was randomized, with a mean interoddball interval of 12 s and a range of 8.2 s.

Two sets of grayscale visual stimuli were used in the experiment. A pair of novel objects (courtesy of Pepper Williams, University of Massachusetts, Boston) was used for nine of the subjects, while 15 familiar objects (e.g., car, chair) were used for the remaining 11 subjects. Novel objects were used to ensure that the effects could be obtained regardless of semantic/verbal influences. In addition, the novel objects could appear in two different locations while the familiar objects could appear in one of 15 positions on the screen. For the familiar object set, one particular object at a particular position served as the standard, and the 14 other objects and locations served as oddballs, with no repeat of oddball identity or position in an fMRI run. The same object and location were used as standard for the entire fMRI session. For half of the subjects, the standard location was the point vertically below the fixation cross, and for the other half, it corresponded to the point vertically above the fixation. All subjects were right-handed, but nine of them used their left hand to respond while the remaining used their right hand. Except for one brain region (see below), no obvious systematic difference was found for these factors (number/type of oddballs and hand used), and the data were pooled across groups to increase statistical power of the pixel-based analysis, with subjects as a random factor. The regions of activation thereby identified in experiment 1 could then serve as the basis for a region of interest (ROI) analysis for the other experiments. The effect of hand used was also analyzed separately (see Results) and found to affect only the left parietal activation.

Stimuli were displayed on an LCD panel and back-projected onto a screen positioned at the front of the magnet. Subjects viewed this display through a mirror mounted above their eyes. Stimuli were presented with PSYSCOPE software (Cohen et al., 1993) running on a Macintosh Power PC. A digital interface enabled the Macintosh to record when each image was acquired, and this information was used to synchronize the stimuli presented with the image acquisition to high accuracy (Robson et al., 1998).

FMRI Methods
Imaging was performed on a GE 1.5 T Sigma (Milwaukee, WI) scanner with an ANMR (Advanced NMR, Wilmington, MA) resonant gradient echoplanar imaging system. All images were acquired using a standard quadrature head coil and a T2*-sensitive gradient-recalled single-shot echoplanar pulse sequence. Ten contiguous coronal T1-weighted slices covering the posterior half of the brain (from occipital pole to central sulcus) were prescribed based on sagittal localizers acquired at the beginning of each scanning session. Functional T2*-weighted images were acquired at the same locations in runs of 1020 images (102 per slice). FMRI acquisition parameters were as follows: repetition time (TR) of 1650 ms, echo time of 60 ms, flip angle of 60°, acquisition matrix of 128 × 64, and field of view of 40 × 20 cm. Voxel resolution was 3.12 × 3.12 mm in plane and 7 mm thick.

Data Analysis
Before data analysis, functional images showing excessive motion (more than 0.5 pixel over the entire run) or other artifacts (such as ghosting) were removed from the analysis. SPM96 algorithm was used to correct for motion between successive images in each run.

Data from each individual subject were processed using a pixel-based temporal correlation analysis. The time course data of each pixel were first averaged across trials for each oddball type. The resulting average waveform was cross-correlated with an estimated time course using a hemodynamic response function (HRF) defined from a previous study from this laboratory (Robson et al., 1998). This estimated response was a gamma-variate function of the form:

$$\mathrm{HRF} = (t - t_0)^{\alpha}\, e^{(-(t - t_0)/\beta)}$$
$$\text{where } t_0 = -0.25,\ \alpha = 14,\ \beta = 0.344$$

The correlation coefficient r for each voxel was calculated, and color-scaled r values were overlaid on the T1-weighted images.

The anatomical and gaussian-filtered (full width at half maximum = 6.3 mm) BOLD images for each subject were then transformed into the standardized Talairach atlas coordinate system (Talairach and Tournoux, 1988) using eight anatomical anchor points (AC, PC, and the superior, inferior, anterior, posterior, left, and right most points on the cortical surface). The resulting maps from all subjects were superimposed to create composite maps. Statistical maps of group composites were derived using a bootstrapping randomization technique. Under the null hypothesis of no correlation, the expected value for a comparison is equal to zero. The randomization creates a population distribution for each voxel by calculating randomized values for the comparison in which randomly chosen subsets of subjects' data get reversed contrast weights. The randomization was performed 2000 times in order to generate a sampling distribution. The composite maps were first cluster-filtered (nine contiguous pixels) and thresholded to reveal only pixel clusters with r values that fall above the 99.5 percentile of the random sampling distribution.

A contrast analysis was performed to directly compare the activation in the location and identity oddballs. Sites were considered significantly activated if they survived $p < 0.005$ (uncorrected) for regions that were previously activated in the single oddball conditions.

Experiment 2
In order to compare the location, identity, and conjunction of location and identity oddballs directly, we performed another experiment with all three types of oddballs in every fMRI run.

Task Design
As in experiment 1, except that only the set of 15 familiar objects was used. There were 14 oddballs per run (five each of two types and four of the third type, counterbalanced between runs).

Data Analysis

The statistical significance was assessed with an ROI analysis, with ten ROIs based on the activation patterns obtained in experiment 1. The drawing of the ROI boundaries was guided by the activation peaks in the group composites and aided by examination of each subject's data. A given ROI was considered significantly activated if its mean Z-score across subjects was significantly different from zero, as assessed by a t test ($p < 0.05$), using a Bonferroni correction. Hemispheric differences were also directly analyzed within each ROI, and a distinction is made between left and right hemisphere activation only if the test revealed statistical significance.

A pixel-based analysis was also performed to provide convergence and to visualize the different pathways. This pixel-based approach was applied not only to the standard correlational analysis as described in experiment 1, but to a mean signal intensity analysis as well. For the signal intensity analysis, activation associated with the estimated peak of the response (images acquired at 3.3–6.6 s after stimulus presentation) was compared to the activation associated with the rising and falling phases of the response (0–1.65 s and 8.25–9.9 s). The composites of the resulting statistical parametric maps were computed as described for experiment 1 and thresholded at $p < 0.05$.

Experiment 3

Task Design

Subjects performed a difficult target-monitoring task at fixation while an object was infrequently presented in the peripheral visual field. The central task consisted of covertly counting the number of iterations of a black target letter (about 1° of visual angle) presented among a rapid sequence of visual distractors (other letters). Stimulus duration was 150 ms with no interstimulus interval. The number of targets varied between runs from 42 to 58. Every 12 s during the 202 s long rapid serial presentation, a black peripheral stimulus (wheel) was shown for 150 ms at one of the four cardinal points of the white screen (object diameter of 5° visual angle, centered about 10° from the central display). No task was performed with the peripheral object. To minimize interference of target performance by the peripheral stimuli, the peripheral object was always presented at least 300 ms before or after a target presentation. The order of presentation of the peripheral object at the four locations was randomized. There were 16 peripheral stimuli per run and 8 runs per subject.

Stimulus generation and presentation was performed with RSVP software (P. Williams and M. J. Tarr, RSVP: experimental control software for MacOS, http://psych.umb.edu/rsvp/). Peripheral object presentations were synchronized with T2*-weighted image acquisition as discussed above.

FMRI Methods and Data Analysis

Imaging parameters were identical to those in experiments 1 and 2 with the following exceptions: TR = 2000 ms, 101 images/slice. Data analysis was performed using the pixel-based approach as described in experiment 1 for visualization and the ROI approach as described in experiment 2 for assessment of statistical significance.

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