Published in final edited form as:

Neuroimage. 2008 October 1; 42(4): 1686–1697. doi:10.1016/j.neuroimage.2008.06.016.

VISUOSPATIAL CONTEXTUAL PROCESSING IN THE PARIETAL CORTEX: AN FMRI INVESTIGATION OF THE INDUCED ROELOFS EFFECT

Elizabeth Walter and Paul Dassonville

Department of Psychology and Institute of Neuroscience, University of Oregon

Abstract

Neighboring contextual elements can dramatically affect the manner in which the brain processes the perceptual characteristics of an object. Indeed, many well-known visual illusions rely on misleading contextual cues to create misperceptions of size, length or orientation (e.g., in the Ebbinghaus, Muller-Lyer or rod-and-frame effect, respectively). However, little is known about the brain regions underlying these integrative computations. The current study used fMRI to delineate the brain areas responsible for processing visuospatial contextual information. Participants were asked to determine whether a small target was positioned left or right of midline in the presence of an offset rectangle designed to induce a shift in the participant's perception of straight-ahead (the induced Roelofs effect). We found localized, bilateral regions in superior parietal cortex and precuneus that were specifically active when participants judged the target location in the presence of this shifted context; significantly less activation was present when a color judgment was made with identical stimuli, or when the location judgment was made without a Roelofs-inducing frame. We propose that this portion of parietal cortex is selectively involved in processing visuospatial contextual information. Additional findings support the notion that perceptual judgments of target location based on an egocentric frame of reference fall within the purview of the dorsal stream of visual processing, rather than the ventral stream.

Keywords

parietal cortex; two visual systems hypothesis; Roelofs effect; color perception; space perception; egocentric; allocentric

Introduction

When perceiving and judging attributes such as the size, orientation or location of an object, other elements in the visual scene are often unconsciously taken into account by the observer. Well-documented illusions such as the Ebbinghaus illusion (Wundt, 1898), Müller-Lyer illusion (1889), and the rod-and-frame effect (Witkin and Asch, 1948) rely on extraneous cues to mislead our perceptual system about certain aspects of an attended object. Although visuospatial contextual integration is a factor in many perceptual tasks, few studies to date have

Correspondence: Paul Dassonville, Dept. of Psychology, 1227 University of Oregon, Eugene, OR 97403, (541) 346-4956, prd@uoregon.edu.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

explicitly addressed its neural underpinnings (though see Weidner and Fink, 2006; Murray et al., 2006). The current imaging study sought to uncover the neural locus of visuospatial contextual processing in an illusion known as the induced Roelofs effect (Bridgeman et al., 1997). In this illusion, observers in a darkened environment tend to misperceive the location of a target object when it is presented in the context of a large rectangular frame whose center is positioned left or right of the observer's midsagittal plane. For example, a left-shifted frame will cause an enclosed target to appear to lie further to the right, and vice-versa. Though the illusion was initially described by Bridgeman et al. (1997) as resulting from competition between separate allocentric and egocentric frames of reference, the effect has more recently been shown to be the specific result of a distortion of egocentric space. In this updated view (Dassonville et al., 2004; Dassonville and Bala, 2004), the induced Roelofs effect causes the observer's egocentric reference frame to be pulled in the direction of the large rectangle. Indeed, when the observers are asked to "look straight ahead," the offset frame biases their reports toward the center of the rectangle. Thus, when a target's location is encoded within the observer's biased reference frame, it appears to be displaced in the opposite direction of the rectangular frame.

In the paradigm of the present study, participants were instructed to attend to and report either the location or color of a small target square. In half of the trials, the target was presented alone on a black background. For the remaining half, the target was presented inside a large, colored frame offset from the participant's midline. The context of this larger frame served to induce the Roelofs effect, as well as a color contrast effect (i.e., a red frame caused the target to be perceived with more of a greenish tint and vice versa; Webster et al., 2002). As the low-level aspects of the stimuli were identical across the location and color judgments, any observed differences in brain activation could be attributed to the specific judgments made concerning particular aspects of the target (e.g., noting position during the location judgment, and hue during the color judgment). The results provided an opportunity to assess the regions responsible for contextual processing in the two tasks.

Weidner and Fink (2006) have previously examined visuospatial contextual processing in a task that involved a visual illusion, the Müller-Lyer illusion. Their findings suggest that the superior parietal and lateral occipital cortices play a role in visuospatial contextual processing. Given this, it might also be expected that the same areas are responsible for the contextual processing that leads to the Roelofs illusion. On the other hand, it might be expected that the contextual processing involved in a length judgment task (such as that in the Landmark task employed by Weidner and Fink, 2006) is different from that involved in an egocentric location task such as the one used here. Indeed, a previous study from our lab (Walter et al., submitted) assessed individual differences in susceptibilities to these illusions, and found evidence that they were driven by separate underlying mechanisms. Given this, we predicted that the pattern of activation associated with contextual processing in the Roelofs illusion will differ substantially from that of the Müller-Lyer illusion.

The results of this study also allowed us to evaluate the utility of two major characterizations of function for the separate streams of visual processing, referred to henceforth as the "what vs. where" (Ungerleider and Mishkin, 1982) and "perception vs. action" hypotheses (Milner and Goodale, 1995). For example, the what vs. where framework suggests that there is a ventral stream of visual areas that is responsible for processing the visual information necessary for determining the identity of a viewed object, and a dorsal stream responsible for determining the object's location in space (Ungerleider and Mishkin, 1982). Within this framework, then, we would expect a predominantly ventral pattern of activation during the trials that require a color judgment, and a dorsal pattern during the trials that require a location judgment. The perception vs. action framework, on the other hand, suggests that the ventral stream is responsible for processing the visual information that leads to our perception of the objects

that populate the visual world, whereas the dorsal stream is responsible for guiding actions (e.g., reaches, pointing movements, eye movements) toward these objects (Milner and Goodale, 1995). Both of the tasks employed here were perceptual in nature, in that they involved a perceptual judgment that was expressed with a symbolic button press (rather than an isomorphic goal-directed response aimed directly toward the stimulus itself). Thus, the perception vs. action framework leads to the prediction that both the color and location judgments will give rise to a predominantly ventral pattern of activation.

Materials and methods

Participants

Sixteen right-handed participants (10 females; 18 – 32 years of age) gave their informed, written consent as per the University of Oregon Institutional Review Board. Participants were compensated either with money or course credit for an introductory psychology course, and were naïve to the goals of the study. An initial behavioral calibration session took approximately one hour, while the scanning session itself lasted 1.5 – 2 hours.

Stimuli

During each trial, participants were presented with a small colored target ($0.5^\circ \times 0.5^\circ$ square). All targets appeared to be yellowish in color, with a hint of either red or green (see below). The target was presented either alone (on a black background; Figure 1e) or in the presence of an offset, colored frame (16° horizontal $\times$ 8° vertical). Frames were centered at one of four locations (1.6° or 4.8° left or right of the participant's midsagittal plane) to induce a Roelofs distortion of the target's perceived location, and in one of four colors (RGB = 170, 85, 0; 142, 113, 0; 113, 142, 0; or 85, 170, 0) to induce varying color-contrast effects in the target (Figure 1a – d). Like the frame colors, target colors fell along a color space continuum from red to green, defined by 1) requiring the red and green RGB components to co-vary, with the sum of these components always adding to 255, and 2) including no blue component (see the *Behavioral calibration* section, below, for a detailed description of the mechanism used to select target colors and locations for each participant).

Experimental tasks

During the majority of the functional imaging runs, participants were asked to judge either the position (left or right of the participant's midline) or the color (tinted red or green) of the small target. The four tasks were organized in a two-by-two design: Task (Location or Color) crossed with Frame (whether the target is presented with or without a frame). During the Color task, the participant was asked to report whether the “yellowish” target was slightly more red or more green. During the Location task, participants indicated whether the target was presented to the left or right of “straight ahead.” In order to ensure that participants relied on egocentric cues during the Location task, we made the scanner room as dark as possible (turning off all lights, covering illuminated monitors, covering the viewing window of the scanner room, dimming the projector and inserting a 64x neutral density filter over the projector lens to eliminate light scatter) so as to eliminate as many allocentric cues as possible.

Participants performed blocks (20 s duration) comprised of 10 trials, alternating with 16 s of rest. Task blocks were preceded by a short (2 s) message reading ‘Left or right?’ or ‘Red or green?’ to indicate to the participant which judgment should be made for trials in the upcoming block. Participants indicated their response with two MR-compatible custom-built button-boxes; a button-press with the left index finger indicated a “left” response during the Location task, and “red” during the Color task, while a press with the right index finger indicated “right” or “green” responses. Each run comprised 12 task blocks (three blocks each of four conditions, in an order randomized separately for each participant), with participants performing 6 – 8

runs. Within each block, the locations and colors of the frames and targets were randomized on a trial-by-trial basis.

Behavioral calibration

Given that activity in the parietal lobe is known to be modulated by the attention required to complete a task (Kastner and Ungerleider, 2000), we attempted to equate all of our tasks for difficulty. To achieve this, we conducted an initial behavioral assessment of each participant in the fMRI scanner, with all viewing parameters (e.g., ambient luminance, projector and viewing settings, position of participant) identical to those used during the subsequent functional scans. During this pretesting period, participants performed location and color judgments identical to those required in the eventual scanning session, with the same frame locations and colors. However, the range of the locations and colors for the targets were varied in an adaptive way, so as to map out the psychometric functions for the location and color judgments when viewing targets in isolation (that is, in the Without-frame conditions), as well as in the presence of each combination of frame location and color in the Within-frame conditions. Participants first performed the Location task (using all combinations of frame location and color), with a wide range of target locations used to ensure a bracketing of the center point of the psychometric function for each frame location (presented in random order). Graphic representations of the psychometric functions were created online, and were used to assess the target locations for the different frames, with the target locations then manually adjusted to focus in on the extent of each psychometric function (that is, to maximize the data collected for the rise of each psychometric function). After the functions for the location judgments were determined, a similar routine was used to determine the psychometric functions for the Color task.

The psychometric functions determined in this way were then used to select stimulus parameters (target location and color) for the subsequent imaging session. In the location judgment, the functions were first characterized by fitting to the data the curve

$$\text{Proportion of "Right responses"} = e^{(\text{Loc} - \text{PSE}) / \text{Slope}} / (1 + e^{(\text{Loc} - \text{PSE}) / \text{Slope}}) \quad (\text{eqn. 1})$$

with Loc equal to the target location, PSE (the point of subjective equality) equal to the location at which the target was reported as being “Left” or “Right” in equal proportions, and Slope characterizing the rate of rise in the psychometric function. A least-squares fitting routine was used to determine the PSE and Slope parameters. These parameters were used to select target locations that occupied equivalent positions (i.e., distances of one and three times the value of the Slope parameter from the PSE) on each psychometric curve for different frame locations in the individual participants (Figure 1f). An analogous procedure was used to select target colors (with the red and green RGB components always summing to 255) for the different frame colors (Figure 1g). These target locations (ranging from 2.4° left to 2.9° right of the participant’s midsagittal plane) and colors (ranging, in RGB values, from 78, 177, 0 to 156, 99, 0) were then used during the functional scans in an attempt to equate the difficulty of each of the four tasks for each participant, thus reducing the possibility of activations related simply to differences in task difficulty or attention levels. After the scans were complete, participants were asked to rate the subjective difficulty of each of the tasks on a scale from 1 = extremely easy (i.e., no effort was required), to 10 = extremely difficult (i.e., required every bit of mental effort that could be mustered).

Quantifying the behavioral effects

To determine the magnitude of the Roelofs effect, psychometric functions (eqn. 1) were fit to the behavioral responses for each frame location (with the behavior expressed as the proportion of “Right” responses for each target location). A one-way ANOVA (SPSS 16.0) was used to

test for a main effect of frame position, and a linear regression was then used to determine the relationship between frame location and the target PSE. The slope of this regression provided a measure of the induced Roelofs effect, which was then expressed as a percent gain. An analogous method was used to determine the gain of the color contrast effect, reflecting the change in the target color PSE associated with the location of the frame color in the red-green color space defined above.

Eye movement localizer task

To account for functional activations caused merely by possible differences in patterns of eye movements in the different tasks, an eye movement localizer task was carried out with a subset of participants. In an additional run, this subset of participants ($n = 9$) made eye movements to small targets ($0.5^\circ \times 0.5^\circ$, 1 s duration each, no ISI) that appeared on a black background, during 20 s blocks separated by intervening periods of rest (16 s). So as to ensure that the cortical oculomotor regions of the brain were fully activated in the eye movement localizer task, targets were displaced at a faster rate, and included more peripheral positions on the screen (and therefore required a wider range of saccade amplitudes) than those presented during the Location and Color tasks. Eye-movement blocks were preceded by 2 s of the instruction "Follow target." Participants were instructed to foveate each target during the movement blocks, and lay still with their eyes open, but without making eye movements, during the rest periods.

Scan parameters and image processing

Functional MR images were acquired using a 3T head-only MRI (Siemens Magnetom Vision, Erlangen, Germany), with a standard birdcage head-coil. For each functional run, we used a standard BOLD (blood-oxygenation-level-dependent) gradient-echo echo-planar imaging sequence (TR = 2 s, TE = 30 ms, 32 slices, 4 mm thickness, 0 mm gap, FOV = $200 \times 200 \times 128$ mm) allowing us to achieve nearly whole-brain coverage with a functional in-plane resolution of $3.125 \times 3.125 \times 4$ mm. In addition, we collected anatomical images (whole brain, 1 mm slices, 0 mm gap) using a standard Siemens MPRAGE sequence allowing detailed reconstruction of anatomy with a voxel resolution of $1 \times 1 \times 1$ mm.

All raw functional data from each participant was converted into BrainVoyager 2000 and Brain Voyager QX format (Brain Innovation, Maastricht, The Netherlands) and pre-processed using custom MatLab scripts to automate and standardize image processing. Images were preprocessed by first performing slice-time scan correction and then 3-D motion correction using BrainVoyager. They were then subjected to a temporal high-pass filter to remove the 1st, 2nd and 3rd order elements, and a low-pass spatial filter using a Gaussian kernel (4 mm full-width at half-maximum). Finally, the functional images from each participant were each aligned to the participant's own anatomical scan, which were then aligned with the AC-PC plane and converted into the Talairach atlas space as defined by Talairach and Tournoux (1988) by individually defining bounding boxes for the entire brain, using AC and PC set as anchor points for the transformation (BrainVoyagerQX 1.9). Data from all participants were combined and analyzed using a random-effects general linear model. Models for each block-type during the functional runs were constructed as box-car functions convolved with the hemodynamic response as implemented in the BrainVoyagerQX 1.9 statistical package. We then calculated beta-weights for each voxel, for each condition, to use in later contrasts. We report the areas of activation for each contrast that reached significance with a voxel-level threshold of $p < 0.001$ (uncorrected) then cluster-corrected to an extent threshold of $p < 0.05$, unless otherwise stated. Cluster-based corrections were performed using the Cluster-level Statistical Threshold Estimator plug-in for BrainVoyagerQX 1.9 (Goebel, Esposito and Formisano, 2006).

Results

Behavioral effects

Based on the results of earlier examinations of the Roelofs effect, it was expected that the location of the frame would affect the perceived location of the target, with, for example, left-shifted frames causing a rightward bias in the participant's perception of the target location. Indeed, a significant effect of frame location was seen in the Location task during pre-testing sessions ($F(4, 60) = 5.041, p < 0.005$, with a significant linear contrast, $F(1, 15) = 7.610, p < 0.05$; average gain of 3.0%), and a similar effect was seen during the fMRI scanning sessions ($F(4, 60) = 2.689, p < 0.05$, with a marginal linear contrast, $F(1, 15) = 3.240, p = 0.09$; average gain of 2.8%). During the Color task, a clear color-contrast effect was seen, with the red frames causing a greenish tint in the targets, and vice-versa, in both the pre-testing sessions ($F(4, 60) = 57.856, p < 0.001$, with a significant linear contrast, $F(1, 15) = 63.444, p < 0.001$; average gain of 34%) and the fMRI scanning sessions ($F(4, 60) = 46.667, p < 0.001$, with a significant linear contrast, $F(1, 15) = 82.088, p < 0.001$; average gain of 39%).

According to the post-scan subjective difficulty ratings (Figure 2), participants reported the Location and Color judgments without a frame present as easiest ($M = 3.97 \pm 0.51$ s.e.; $M = 4.69 \pm 0.49$, respectively) and the Location and Color judgments with a frame present as slightly more difficult ($M = 5.78 \pm 0.41$; $M = 5.50 \pm 0.45$, respectively). A 2×2 repeated measures ANOVA of Task (Location and Color) by Frame (With-frame and Without-frame) indicated no difference in perceived difficulty across Location and Color conditions, though there was a statistically significant overall difference between With-frame and Without-frame conditions ($F(1, 15) = 14.731, p < 0.005$). In addition, there was a significant interaction of Task by Frame ($F(1, 15) = 4.768, p < 0.05$). Post-hoc t-tests indicated that this interaction was driven by a significant difference between the Location-with-frame and Location-without-frame conditions ($t(15) = 6.797, p < 0.001$), with no significant differences in the difficulty ratings of other combinations of conditions.

Main effect of the frame

In a random-effects model with all sixteen participants, a contrast of both With-frame conditions versus both Without-frame conditions allowed us to determine which areas were activated merely by the presence of the frame, regardless of the subsequent decision to be made (Figure 3). Not surprisingly, the primary activations were found bilaterally in early visual areas, in the thalamus, middle occipital gyrus (BA 17/18), and lingual gyrus of the occipital lobe (BA 18). Other areas significantly more active with the frame present were found near the parahippocampal gyrus in the occipital lobe (BA 37). In addition, portions of superior parietal cortex (BA 7/19) were significantly activated in this contrast, though this activation appeared to be driven almost entirely by the Location-with-frame condition.

Main effect of the task

To delineate areas of the brain that are generally involved in processing location or color information, a contrast of both Location tasks (With- and Without-Frame) versus both Color tasks was performed (Table 1 and Figure 4). Bilateral regions in the parietal lobe, including superior parietal cortex (BA 7) and right supramarginal gyrus (BA 40) as well as areas in the frontal lobe (right precentral gyrus and left middle frontal gyrus, BA 6) were found to be more active during the Location judgments. In addition, smaller regions of occipital (bilateral superior occipital gyrus, BA 19) and temporal cortices (right middle temporal gyrus, BA 37/39) were also significantly activated in the Location conditions relative to the Color conditions.

In contrast to the dorsal pattern of regions more active in the Location task, the Color task activated ventral regions, including the right fusiform gyrus (BA 20), left lingual gyrus and right inferior occipital gyrus (BA 18).

Task x frame interactions (Roelofs-contrast and color-contrast effects)

The 2×2 design of the experimental paradigm allowed not only a quantification of the main effects of task and frame, but also of any task x frame interactions that would delineate brain regions that more specifically processed the contextual information of the frame for use in a given task. Although there were no cortical regions that showed this pattern of activation when tested with a whole-brain voxel-level threshold of $p < 0.001$ (uncorrected) and then cluster-corrected with an extent threshold of $p < 0.05$, a conjunction analysis of two separate contrasts did isolate regions that showed a sensitivity to both the task and the presence of the frame. First, a Location-with-frame vs. Location-without-frame contrast was used to delineate areas that were involved in processing the visual image of the frame and its related contextual information. A second contrast of Location-with-frame vs. Color-with-frame was used to delineate the areas specifically involved in the location judgment (this contrast also effectively subtracted out the activation associated with, for example, the low-level visual processing of the frame's image, which would presumably be equal in the Location-with-frame and Color-with-frame tasks). The conjunction of these two contrasts yielded those areas that were involved in processing the contextual information provided by the frame during a location judgment. This conjunction, termed the Roelofs-contrast, found activations in right superior parietal cortex (SPL, BA 7) and bilaterally in the precuneus (BA7; Table 1 and Figure 5). Furthermore, an ROI-based analysis of these regions indicated that the activations of the right SPL and precuneus do reflect a task x frame interaction, with a greater frame-related activation associated with the Location task than with the Color task ($t > 5.728$, $p < 0.0001$). In contrast, the region of activation in left precuneus failed to show a task x frame interaction ($t = 0.788$).

In order to delineate areas that were significantly active during the Color-contrast condition, we performed a conjunction analysis that isolated areas active in both of the following contrasts: (Color-with-frame vs. Location-with-frame) and (Color-with-frame vs. Color-without-frame). No voxels were significantly activated with our predefined whole-brain voxel-level threshold of $p < 0.001$ (uncorrected) cluster corrected with an extent threshold of $p < 0.05$. However, at a slightly more lenient threshold (voxel-level threshold of $p < 0.005$, cluster corrected at $p < 0.05$), regions of activation were seen (Figure 5) in the right fusiform gyrus (BA 20/37), left inferior occipital gyrus (BA 17/18), and left inferior frontal gyrus (BA 6). When tested with an ROI-based analysis, all of these regions did reflect a task x frame interaction ($t > 4.285$, $p < 0.0001$), with a greater sensitivity to the frame during the color task than during the location task.

Eye-movement control task

To rule out the possibility that the pattern of activation in the Roelofs-contrast was due simply to differences in eye movements across these tasks, nine of the participants performed an additional eye movement localizer task. Because our concern in doing this control was to compare activations within our tested group, we performed a fixed-effects analysis of the eye-movement data and compared it with a fixed-effects model of the same participants' Location and Color runs, with all contrasts thresholded at $p < 0.05$ (Bonferroni corrected). During the eye movement localizer blocks, extensive regions of cortex were significantly activated, including the frontal eye fields (FEF; precentral gyrus) and regions in the parietal cortex, with foci near the intraparietal sulcus. In addition, large regions of occipital cortex (BA 17/18) and inferior parietal cortex (BA 40) were also activated during the eye movement localizer. Although some areas active in the Roelofs-contrast overlapped somewhat with areas implicated in the eye movement localizer task (specifically, an area in precuneus, BA 7), the Roelofs-

contrast and the eye movement localizer showed very different task activation profiles overall. Indeed, of all of the voxels active in the Roelofs-contrast, 86% showed no overlap with areas activated during the eye movement task (Figure 6).

Discussion

This study examined the brain areas responsible for judgments of location and color, as well as the areas that are involved in processing contextual cues associated with these judgments. We demonstrated brain activations that were uniquely related to decisions about a target's location versus its color, even when viewing identical visual stimuli. Specifically, judgments regarding location in our paradigm activated a network of parietal and frontal areas, relative to the tasks requiring a decision about color. Furthermore, certain parietal areas (BA 7) were selectively active when making an egocentric location judgment in the presence of contextual information (the Roelofs-contrast). The Color tasks, in comparison to the Location tasks, primarily activated ventral visual areas. In addition, our Color-contrast task (that is, a color decision in the presence of the frame) activated ventral visual areas, primarily in the fusiform and inferior occipital gyri. These sites of color-related activation correspond well to those described in previous imaging studies as being homologues of macaque color processing areas (e.g., Tootell and Hadjikhani, 2001; Hadjikhani et al., 1998). Although the design of this study did allow for an assessment of the brain regions involved in color processing, the goal of the study was to focus on location judgments and the use of visuospatial context; for this reason, issues of color processing will be addressed only briefly throughout the remainder of the Discussion.

Factors influencing behavioral effects

Though we observed a robust color contrast effect, the behavioral induced Roelofs effects exhibited by our participants (an average gain of approximately 3%; that is, an error of 0.144° for a frame shifted 4.8° from the midline) were attenuated relative to the effects typically seen in our lab and that of Bridgeman (with average gains of approximately 8 – 16%; e.g., Dassonville et al., 2004). The reasons for this difference in effect size are unknown, though a number of different factors may have contributed. First, previous investigations of the Roelofs effect in our lab have taken place in complete darkness, preventing the participants from using an allocentric strategy to solve the task, and instead forcing them to rely on egocentric cues. Though we attempted to make the MRI environment completely dark, it was impossible to eliminate all light scatter from the projector (even with a black background color and a 64x neutral density filter covering the lens), which resulted in a faint edge visible around the projection screen. It is possible that the presence of this cue allowed the participants to partially overcome the shift of the apparent midline typically induced by the offset frame, thereby reducing the Roelofs effect. In addition, participants in previous Roelofs experiments have generally completed the task sitting upright, while participants in the current study were lying supine on the scanner gurney as they made their decisions. Although a supine posture in itself does not affect the perception of a target's location in the body-referenced azimuth (Ceyte et al., 2007), there is evidence that suggests that this posture may alter the brain's reliance on the various cues used to define a reference frame for the completion of cognitive tasks (e.g., Marendaz, 1998). It is possible that the supine posture of the participants in the present study caused a devaluation of the cue provided by the illuminated frame, thereby decreasing the magnitude of the Roelofs effect. Another factor that should be considered as a possible reason for the small magnitude of the Roelofs effect was the participants' extensive exposure to the stimuli during the hour-long calibration pre-testing session. However, a smaller than expected effect was already obvious in the data collected during the pre-testing session, suggesting that this was not an inadvertent effect of training.

Though a number of factors may have contributed to the smaller-than-typical Roelofs effect, the fact that an effect was still present suggests that participants were indeed making use of a distorted egocentric reference frame during the Location-with-frame tasks. It is known that there are normal individual differences in illusion susceptibility (e.g., Coren et al., 1976; Coren and Porac, 1987; Walter et al., submitted), and it may be that this particular selection of participants just happened to have susceptibilities smaller than in the general population. If that is the case, then the activations reported here would be conservative estimates of the activations that one might expect in more-typically susceptible individuals.

Possible effects of attention and eye movements

The parietal regions found to be active in the Roelofs-contrast are near regions that have been previously demonstrated to be involved with the control of eye movements (Muri et al., 1996) and attention (Kastner and Ungerleider, 2000); because of this, attempts were made to rule out the possibility that the patterns of activation reported here were caused simply by differences in eye movements and attentional demands in the different conditions. Wojciulik and Kanwisher (1999) found that attention-related parietal activation was more dependent on the level of effort involved in performing a visual task, rather than the details of the precise task being tested. We attempted to rule out task difficulty as an explanation for any differences in activation by tailoring stimuli within each task for each participant (that is, by selecting target location and color parameters that occupied identical locations on the psychometric functions that characterize the different judgments). Though our procedures were relatively successful at equating difficulty across the tasks, some differences in the subjective post-scan ratings of task difficulty did remain (Figure 2). This pattern of subjective difficulty across the participants suggests that brain regions primarily sensitive to difficulty would have the most activation associated with the Location-with-frame task and the least with the Location-without-frame task; although the former was true in the areas delineated in the Roelofs-contrast, the latter was not (see the plots of the time course of activation in Figure 4a – c). In addition, the Color-with-frame task was judged by participants to be equally difficult with the Location-with-frame task. Thus, the contrast of these conditions in the Roelofs-contrast should have eliminated any areas strictly modulated by task difficulty. Indeed, clear differences can be seen in the level of activation for these two equally-difficult conditions (Figure 4a – c), suggesting that the activations in these parietal regions were not simply reflections of task difficulty and attentional demands. Likewise, the perceived difficulties of the Color and Location tasks were not significantly different overall, indicating that the regions of activation associated with these tasks were not simply driven by task difficulty.

An examination of the data from the eye movement localizer yields evidence against the idea that the parietal regions activated in the Roelofs-contrast were merely the parietal eye fields, with activations that simply reflected different patterns of eye movements in the different Location and Color tasks (Figure 6). The activation of the Roelofs-contrast was found to have very little overlap with the parietal regions that were active in a task specifically designed to delineate regions involved in oculomotor control. Additionally striking in this regard is the *absence* of other well-known oculomotor regions in those areas activated in the Roelofs-contrast. For example, if the Roelofs-contrast simply reflected a confound in the patterns of eye movements associated with the different tasks, one would also expect to see the frontal eye fields active with this contrast. However, while the frontal eye fields are clearly reflected in the data of the eye movement localizer task, they were not activated in the Roelofs-contrast.

Visuospatial contextual processing

The induced Roelofs effect is only one of many illusions that are brought about by the brain's occasionally inappropriate use of visuospatial contextual cues. However, previous studies have indicated that the mechanisms by which these cues are processed are not necessarily uniform

across the different illusions (e.g., Dyde and Milner, 2002). Previous work in our lab has examined individual differences in susceptibilities to a battery of illusions, and found evidence for subsets of illusions that differ in their underlying mechanisms (see also Coren et al., 1976; Coren and Porac, 1987). For example, susceptibility to the Roelofs effect was found to correlate with the susceptibilities to the rod-and-frame, Ponzo, Poggendorff and Zöllner illusions, while it was unrelated to Müller-Lyer and induced motion susceptibilities (Walter et al., submitted). The grouping of the Roelofs, rod-and-frame, Ponzo, Poggendorff and Zöllner illusions fits well with the hypothesis of Prinzmetal and colleagues (Prinzmetal and Beck, 2001; Shimamura and Prinzmetal, 1999) that a subset of illusions are caused by context-related distortions of the observers perceptual reference frame.

Given the evidence that the induced Roelofs effect is driven by a distortion of the observer's reference frame (Dassonville and Bala, 2004; Dassonville et al., 2004), we predicted that the network of brain structures responsible for processing the contextual cue that drives the distortion would be substantially different from the network of structures responsible for processing visuospatial illusions that are driven by different mechanisms (e.g., the Müller-Lyer illusion). Weidner and Fink (2006) examined the neural mechanisms underlying the Müller-Lyer illusion, and found that the illusion was associated with an increased activation in bilateral lateral occipital cortex as well as the right superior parietal lobule. Interestingly, the superior parietal region delineated in their study was very similar to that demonstrated in the present study with the Roelofs-contrast.¹ Thus, it may be that this portion of the superior parietal region is responsible for processing a wide variety of visuospatial contextual cues, with other brain regions responsible for using the output of this region in a manner suitable for the task being performed. For example, the lateral occipital cortex could use this contextual information from the superior parietal lobule for length judgments that are prone to the Müller-Lyer illusion (Weidner and Fink, 2006), while the frontoparietal network of regions involved in the present Location task could use it for location judgments that are prone to the Roelofs effect.

Implications for the two visual systems hypothesis

With respect to the dorsal and ventral streams of visual processing, the general pattern of activation associated with the Location tasks was predominantly dorsal, and was strikingly different from the more ventral pattern of activation associated with the Color tasks. Indeed, the most ventral of the regions associated with the Location tasks was in the middle temporal gyrus, with Talairach coordinates roughly similar to, and certainly no more ventral than, those from previous descriptions of the motion sensitive areas of V5/MT+ (Watson et al., 1993; Dumoulin et al., 2000; Wilms et al., 2005)², which are generally considered to be components of the dorsal stream of processing (Ungerleider and Pasternak, 2004; Young, 1992). This combination of dorsal activation in the Location tasks and ventral activation with the Color tasks corresponds well to a what vs. where division of labor between these visual processing streams, as proposed by Ungerleider and Mishkin (1982). Furthermore, the finding of robust activation in parietal cortex during the location judgment, coupled with a *lack* of activation in ventral stream areas during that task, runs counter to the proposal of a perception vs. action division of labor, as put forth by Milner and Goodale (1995). According to their characterization, the dorsal stream of visual processing is recruited for guiding goal-directed actions, whereas the ventral stream subserves conscious perceptions about our visual world.

¹Whereas the SPL region in the current study had Talairach coordinates of X = 17, Y = -65, Z = 53, the corresponding region of Weidner and Fink (2006) was centered at X = 16, Y = -68, Z = 55 (after translating their MNI coordinates into the coordinates of Talairach and Tournoux, 1988, using the method of Lacadie et al., in press; <http://www.bioimagesuite.org/Mni2Tal/index.html>).

²The slightly more anterior location of the regions reported in the present study (Talairach y = -51 to -57, compared to the mean y = -67 to -70 from across a number of studies of V5/MT+, as reported by Wilms et al., 2005) might suggest that these regions correspond more specifically to the human analog of MST, which has been reported to be located just anterior to MT (Dukelow et al., 2001). This activation may have been associated with an attempt by participants to use the induced motion of the frame and target from one trial to the next as a partial cue for determining the target's location.

Since both the Location and Color tasks of the present study required perceptual judgments and symbolic button-press responses, the perception vs. action model would have predicted a predominantly ventral activation for both, which was clearly not the case.

Egocentric versus allocentric reference frames

Although our results are broadly consistent with a what vs. where division of function, it is also possible that our findings may be better understood with respect to the particular frame of reference used to complete each of our tasks. Certain computations are most efficiently accomplished using a particular reference frame. For example, a system mediating actions in the world would need a continually updated representation of a target object with respect to one's own limb (or trunk). This representation would not need to be long-lived, but would need to be quickly updated to account for movements of the individual and of objects in the environment. In contrast, a system capable of remembering and classifying objects would need to encode their representations in some more enduring format – perhaps with respect to other items, or to the world in general (e.g., based on gravity or the horizon). In short, it is thought that the parietal cortex codes for space in a variety of egocentric frames (e.g., Colby and Goldberg, 1999; though see Snyder et al., 1997), while visual processing in the temporal lobe organizes objects according to their own spatial interrelationships (i.e., in an allocentric manner, such as the Cognitive Map theory proposes for the hippocampus; O'Keefe and Nadel, 1978). This way of parsing function is rather different from a what vs. where dichotomy, since computations of “where” can be completed in either an egocentric or allocentric reference frame, depending on the circumstances and task requirements. It also differs from an action vs. perception dichotomy, since both perceptions and actions can be driven by either allocentric or egocentric information, depending on the circumstances (Smeets et al., 2002).

Previous functional imaging studies have indeed provided evidence for an egocentric vs. allocentric dissociation of function across the two visual processing streams. Galati, Vallar and colleagues (Vallar et al., 1999; Galati et al., 2000) performed two imaging studies involving egocentric spatial perceptions that dovetail well with the sites of interest found in our Location task. In the earlier study, Vallar et al. (1999) asked participants to note when a bar moving horizontally across a computer screen either changed direction (an allocentric or world-centered judgment), or when it crossed the participant's subjective median plane (an egocentric judgment). In short, these researchers found increased activation in a primarily right-lateralized network of frontal and posterior parietal regions during performance of the egocentric task relative to the allocentric judgment (Vallar et al., 1999). Importantly, they did not find activations sensitive to the egocentric task in any of the ventral stream areas (i.e., in the temporal cortex), even though theirs was a perceptual task. A second imaging study (Galati et al., 2000) again probed egocentric versus allocentric differences, and compared them to a non-spatial task. In this later study, Galati and colleagues (2000) asked participants to view a long, horizontal bar segmented by a shorter, vertical green line. Depending on the condition, participants were asked to indicate the location of the vertical line with respect to their egocentric perception of straight ahead (the egocentric task), to determine the location of the vertical line with respect to the horizontal line that it crossed (the allocentric task), or to judge the relative colors of the lines (the non-spatial task). Although it can be difficult to ascertain the extent of activated clusters, the sites determined in the present study to be associated with the Location tasks do appear to overlap with sites of activation for the egocentric task of Galati et al. (2000). In particular, we find overlap in right posterior parietal (precuneus, BA 7) and left frontal cortex (middle frontal gyrus/precentral sulcus; BA 6).

Summary

The current study found that portions of posterior parietal cortex (BA 7) were selectively active when making decisions about the location of a target in the presence of contextual information. Though located in posterior parietal cortex, these areas are distinct from regions that are directly related to eye-movement and attentional shifts. This provides support for the idea that the function of these parietal areas extends beyond egocentric transformations and spatial attention, and includes a role in processing the visuospatial contextual information that, under specific circumstances, can lead to visuospatial illusions. The pattern of activation seen during location judgments also supports a dissociation of ventral and dorsal processing streams based on the neural mechanisms involved in judging the identity or location of a target, respectively (Ungerleider and Mishkin, 1982), or perhaps the mechanisms involved in encoding locations within allocentric and egocentric reference frames, respectively (e.g., Vallar et al., 1999; Galati et al., 2000).

Acknowledgements

We thank Scott Watrous and Mark Dow for technical support throughout this study. This work was derived from a portion of the doctoral dissertation of Elizabeth Walter, and was partially supported by an NIH Systems Physiology Training Grant (5-T32-GM07257) to EW and an award from the Telemedicine and Advanced Technology Research Center (DAMD17-01-1-0750). Preliminary results were presented at the 2006 Annual Meeting of the Vision Sciences Society.

References

- Bridgeman B, Peery S, Anand S. Interaction of cognitive and sensorimotor maps of visual space. *Perception and Psychophysics* 1997;59:456–469. [PubMed: 9136275]
- Ceyte H, Cian C, Nougier V, Olivier I, Trousselard M. Role of gravity-based information on the orientation and localization of the perceived body midline. *Experimental Brain Research* 2007;176:504–509.
- Colby C, Goldberg M. Space and attention in parietal cortex. *Annual Review of Neuroscience* 1999;22:319–349.
- Coren S, Girgus J, Erlichman H, Hakstian AR. An empirical taxonomy of visual illusions. *Perception and Psychophysics* 1976;20:129–137.
- Coren S, Porac C. Individual differences in visual-geometric illusions: Predictions from measures of spatial cognitive abilities. *Perception and Psychophysics* 1987;41:211–219. [PubMed: 3575080]
- Dassonville P, Bala JK. Action, perception and the Roelofs effect: A mere illusion of dissociation. *PLoS Biology* 2004;2:1936–1945.
- Dassonville P, Bridgeman B, Bala J, Thiem P, Sampanes A. The induced Roelofs effect: two visual systems or the shift of a single reference frame? *Vision Research* 2004;44:603–611. [PubMed: 14693187]
- Dukelow SP, DeSouza JFX, Culham JC, van den Berg AV, Menon RS, Vilis T. Distinguishing subregions of the human MT+ complex using visual fields and pursuit eye movements. *Journal of Neurophysiology* 2001;86:1991–2000. [PubMed: 11600656]
- Dumoulin S, Bittar R, Kabani N, Baker C, Le Goualher G, Pike GB, Evans A. A new anatomical landmark for reliable identification of human area V5/MT: A quantitative analysis of sulcal patterning. *Cerebral Cortex* 2000;10:454–463. [PubMed: 10847595]
- Dyde RT, Milner AD. Two illusions of perceived orientation: one fools all of the people some of the time; the other fools all of the people all of the time. *Experimental Brain Research* 2002;144:518–527.
- Galati G, Loebel E, Vallar G, Berthoz A, Pizzamiglio L, LeBihan D. The neural basis of egocentric and allocentric coding of space in humans: a functional magnetic resonance study. *Experimental Brain Research* 2000;133:156–164.
- Goebel R, Esposito F, Formisano E. Analysis of functional image analysis contest (FIAC) data with Brainvoyager QX: From single-subject to cortically aligned group general linear model analysis and

- self-organizing group independent component analysis. *Human Brain Mapping* 2006;27:392–401. [PubMed: 16596654]
- Hadjikhani N, Liu AK, Dale AM, Cavanagh P, Tootell RH. Retinotopy and color sensitivity in human visual cortical area V8. *Nature Neuroscience* 1998;1:235–241.
- Kastner S, Ungerleider L. Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience* 2000;23:315–341.
- Lacadie CM, Fulbright RK, Rajeevan N, Constable RT, Papademetris X. More accurate Talairach coordinates for neuroimaging using nonlinear registration. *NeuroImage*. in press
- Lancaster JL, Woldorff MG, Parsons LM, Liotti M, Freitas CS, Rainey L, Kochunov PV, Nickerson D, Mikiten SA, Fox PT. Automated Talairach atlas labels for functional brain mapping. *Human Brain Mapping* 2000;10:120–131. [PubMed: 10912591]
- Marendaz C. Nature and dynamics of reference frames in visual search for orientation: Implications for early visual processing. *Psychological Science* 1998;9:27–32.
- Milner, AD.; Goodale, MA. *The visual brain in action*. Oxford University Press; New York: 1995.
- Müller-Lyer FC. Optische Urteilstäuschungen [Deception of visual judgment]. *Dubois-Reymonds Archive für Anatomie und Physiologie* 1889;263–270. Supplement
- Muri RM, Iba-Zizen MT, Derosier C, Cabanis EA, Pierrot-Deseilligny P. Location of the human posterior eye field with functional magnetic resonance imaging. *Journal of Neurology, Neurosurgery and Psychiatry* 1996;60:445–448.
- Murray SO, Boyaci H, Kersten D. The representation of perceived angular size in human primary visual cortex. *Nature Neuroscience* 2006;9:429–434.
- O’Keefe, J.; Nadel, L. *The Hippocampus as Cognitive Map*. Oxford University Press; New York: 1978.
- Prinzmetal W, Beck D. The tilt-constancy theory of visual illusions. *Journal of Experimental Psychology: Human Perception and Performance* 2001;27:206–217. [PubMed: 11248934]
- Rizzolatti G, Matelli M. Two different streams form the dorsal visual system: Anatomy and functions. *Experimental Brain Research* 2003;153:146–157.
- Roelofs C. Optische Localisation. *Arch Augenheilkunde* 1935;109:395–415.
- Servos P, Osu R, Santi A, Kawato M. The neural substrates of biological motion perception: an fMRI study. *Cerebral Cortex* 2002;12:772–782. [PubMed: 12050089]
- Shimamura AP, Prinzmetal W. The Mystery Spot illusion and its relation to other visual illusions. *Psychological Science* 1999;10:501–507.
- Smeets J, Brenner E, de Grave DDJ. Illusions in action: Consequences of inconsistent processing of spatial attributes. *Experimental Brain Research* 2002;147:135–144.
- Snyder LH, Batista RA, Andersen RA. Coding of intention in the posterior parietal cortex. *Nature* 1997;386:167–170. [PubMed: 9062187]
- Talairach, J.; Tournoux, J. *Co-planar stereotaxic atlas of the human brain*. Thieme; New York: 1988.
- Tootell RH, Hadjikhani N. Where is ‘dorsal V4’ in human visual cortex? Retinotopic, topographic and functional evidence. *Cerebral Cortex* 2001;11:298–311. [PubMed: 11278193]
- Ungerleider, L.; Mishkin, M. Two cortical visual systems. In: Ingle, DJ.; Goodale, MA.; Mansfield, RJW., editors. *Analysis of Visual Behavior*. 1982.
- Ungerleider, L.; Pasternak, T. Ventral and dorsal visual processing streams. In: Chalupa, L.; Werner, J., editors. *The Visual Neurosciences*. MIT Press; Cambridge, Mass: 2004.
- Vallar G, Loebel E, Galati G, Berthoz A, Pizzamiglio L, LeBihan D. A front-parietal system for computing the egocentric reference frame in humans. *Experimental Brain Research* 1999;124:281–286.
- Walter E, Dassonville P, Bochsler T. A specific autistic trait that modulates visuospatial illusion susceptibility. submitted
- Watson JD, Myers R, Frackowiak R, Hajnal JV, Woods RP, Mazziota JC, Shipp S, Zeki S. Area V5 of the human brain: evidence from a combined study using positron emission tomography and magnetic resonance imaging. *Cerebral Cortex* 1993;3:79–94. [PubMed: 8490322]
- Webster MA, Malkoc G, Bilson AC, Webster SM. Color contrast and contextual influences on color appearance. *Journal of Vision* 2002;2:505–519. [PubMed: 12678648]
- Weidner R, Fink GR. The neural mechanisms underlying the Müller-Lyer illusion and its interaction with visuospatial judgments. *Cerebral Cortex* 2006;17:878–884. [PubMed: 16707733]

- Wilms M, Eickhoff SB, Specht K, Amunts K, Shah NJ, Malikovic A, Fink GR. Human *V5/MT+*: Comparison of functional and cytoarchitectonic data. *Anatomy and Embryology* 2005;210:485–495. [PubMed: 16328357]
- Witkin HA, Asch SE. Studies in space perception. IV. Further experiments on the perception of the upright with displaced visual fields. *Journal of Experimental Psychology* 1948;38:762–782.
- Wojciulik E, Kanwisher N. The generality of parietal involvement in visual attention. *Neuron* 1999;23:747–764. [PubMed: 10482241]
- Wundt, W. *Die geometrisch-optischen Tauschungen* [The geometric-optical illusion]. Teubner; Leipzig: 1898.
- Young MP. Objective analysis of the topological organization of the primate cortical visual system. *Nature* 1992;358:152–155. [PubMed: 1614547]

Figure 1.

Schematic examples of the stimuli, depicting the locations and colors of the frames and targets in the With-frame (a – d) and Without-frame trials (e). Images are drawn to scale, with the exception of the targets, which are represented here as twice their normal size for clarity. Although the RGB values of the images are the same as those used in the experiment, peculiarities in the printing process have distorted the colors from those seen by the participants. In addition, the figure depicts only 4 of the 16 combinations of four frame locations and four colors. Vertical dashed lines (not seen by participants) represent the location of the participant's midsagittal plane. Curves (f, g) show the best-fit psychometric functions for the Location (f) and Color (g) judgments of a typical participant in the pre-scan behavioral calibration

procedure. Circles represent the target locations and colors used for this participant during the subsequent experimental scans, with the labeled circles depicting the parameters for those targets shown in **a – e**.

Figure 2. Patterns of subjective difficulty for the four tasks, demonstrating a significant main effect of frame and a task x frame interaction.

Figure 3.

Functional maps demonstrating widespread regions in occipital, temporal and parietal cortex that are more active during the With-frame vs. Without-frame conditions. The event-related averaging graphs (bottom panels, corresponding to the labeled arrows in the brain images) show the time course of the activations in the Location-with-frame (red), Location-without-frame (orange), Color-with-frame (dark blue) and Color-without-frame (light blue) conditions. All activations surpassed a whole-brain voxel-level threshold of $p < 0.001$ (uncorrected) with a cluster-corrected threshold of $p < 0.05$.

Figure 4.

Functional maps demonstrating regions that are more active during the Location vs. Color tasks (warm colors), or more active during the Color vs. Location tasks (cool colors). The event-related averaging graphs (bottom panels, corresponding to the labeled arrows in the brain images) show the time course of the activations in the Location-with-frame (red), Location-without-frame (orange), Color-with-frame (dark blue) and Color-without-frame (light blue) conditions. All activations surpassed a whole-brain voxel-level threshold of $p < 0.001$ (uncorrected) with a cluster-corrected threshold of $p < 0.05$.

Figure 5.

Functional maps demonstrating regions that were active in the Roelofs-contrast (a conjunction of the following contrasts: Location-with-frame vs Color-with-frame and Location-with-frame vs Location-without-frame) or Color-contrast (a conjunction of the following contrasts: Color-with-frame vs Location-with-frame and Color-with-frame vs Color-without-frame). The event-related averaging graphs (bottom panels, corresponding to the labeled arrows in the brain images) show the time course of the activations in the Location-with-frame (red), Location-without-frame (orange), Color-with-frame (dark blue) and Color-without-frame (light blue) conditions. Roelofs-contrast activations surpassed a whole-brain voxel-level threshold of $p < 0.001$ (uncorrected) with a cluster-corrected threshold of $p < 0.05$. Color-contrast activations

surpassed a whole-brain voxel-level threshold of $p < 0.005$ (uncorrected) with a cluster-corrected threshold of $p < 0.05$.

Figure 6.

Brain regions showing voxels significantly activated in a fixed-effects analysis of all participants ($n = 9$) who performed the eye movement localizer task, in addition to the Location and Color tasks. Shown in yellow are those areas significantly activated during the Roelofs-contrast. Shown in light blue are those voxels activated during the eye movement localizer task. Shown in green are those regions common to both the Roelofs-contrast and the eye movement localizer task (i.e., overlap areas). All contrasts are threshold at $p < 0.05$, Bonferroni corrected.

Table 1

Results of the random effects analysis ($n = 16$). All contrasts were performed using a whole-brain voxel-level threshold of $p < 0.001$ (uncorrected) with a cluster-corrected threshold of $p < 0.05$, except the Color-contrast condition which used a more lenient voxel-level threshold of $p < 0.005$ (uncorrected) with a cluster-corrected threshold of $p < 0.05$. Each entry refers to the center of mass of a single region of activation, and all Brodmann areas refer to the anatomical region nearest the center coordinate, obtained from the Talairach daemon (Lancaster et al., 2000; <http://www.talairach.org/daemon.html>).

	BA	Anatomical location	Talairach Coordinates*			Extent (mm ³)	average <i>t</i> -value
Location >> Color			x	y	z		
Parietal	7	Right superior parietal	35	-51	51	844	4.63
Parietal	7	Right superior parietal	11	-66	52	5929	4.77
Parietal	7	Left superior parietal	-11	-65	54	3288	4.67
Parietal	40	Right supramarginal gyrus	56	-38	32	873	4.53
Occipital	19	Right superior occipital gyrus	34	-73	27	96	4.26
Occipital	19	Left superior occipital gyrus	-36	-82	24	92	4.38
Temporal	37	Right middle temporal gyrus	51	-51	-2	176	4.48
Temporal	39	Right middle temporal gyrus	47	-57	11	230	4.53
Frontal	4/6	Right precentral gyrus	33	-12	52	86	4.36
Frontal	6	Right precentral gyrus	24	-9	66	330	4.48
Frontal	6	Left middle frontal gyrus	-24	-12	58	390	4.27
Color >> Location							
Temporal	20	Right fusiform gyrus	28	-41	-18	212	4.08
Occipital	18	Right inferior occipital gyrus	34	-88	-3	135	4.21
Occipital	18	Left lingual gyrus	-23	-91	-6	1018	4.40
Roelofs-contrast							
Parietal	7	Right SPL	16	-68	55	95	4.26
Parietal	7	Right precuneus	16	-77	41	1141	4.33
Parietal	7	Left precuneus	-15	-70	50	173	4.24
Color-contrast							
Temporal	20/37	Right fusiform gyrus	30	-42	-15	461	3.66
Occipital	17/18	Left inferior occipital gyrus	-20	-92	-4	1140	3.61
Frontal	6	Left inferior frontal gyrus	-41	1	33	277	3.48

* Locations are reported in the normalized coordinate space of Talairach and Tournoux (1988)