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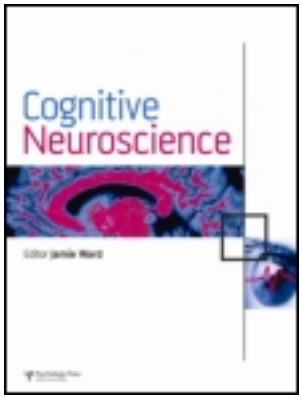

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The role of spatial attention during spatial encoding

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The role of spatial attention during spatial encoding

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In the present fMRI study, we aimed to assess whether spatial encoding is mediated by spatial attention. During encoding, participants were presented with abstract shapes to the left or right of fixation. During retrieval, old and new shapes were presented at fixation and participants classified each shape as "old-left", "old-right", or "new". Subsequently remembered items were assumed to have been attended during encoding, while subsequently forgotten items were assumed to have been unattended during encoding. Mirroring classic spatial attention contralateral extrastriate effects, contralateral subsequent memory effects were observed in extrastriate cortical regions BA18 and BA19 (e.g., encoding-left-hits > encoding-left-misses activated the right extrastriate cortex). An additional individual-trial modeling procedure revealed that 79.35% and 100% of accurately encoded items in the left hemisphere and the right hemisphere, respectively, reflected spatial processing. These results suggest that spatial encoding is largely, but not completely, mediated by spatial attention.

Keywords: Explicit memory; Subsequent memory; Contralateral; Extrastriate; fMRI.

Attention is thought to play an important role during explicit memorial encoding. This view has been bolstered by evidence that encoding produces activity in the frontal cortex and the parietal cortex, regions involved in the control of attention, in addition to the occipital cortex, which reflects sensory attention effects (for a review see, Pessoa, Kastner, & Ungerleider, 2003). Subsequent memory studies, which isolate encoding activity by contrasting later remembered and forgotten items, have reported activity in the parietal and occipital cortex and, based on the overlap with attentional processing regions, have attributed this activity to attention (Sommer, Rose, Weiller, & Büchel, 2005; Sommer, Rose, & Büchel, 2006; Strange, Otten, Josephs, Rugg, & Dolan, 2002; Uncapher, Otten, & Rugg, 2006). Attention has also been directly manipulated during encoding and a greater degree of attention has been associated with a higher magnitude of activity in the prefrontal and parietal cortex (Kensinger, Clarke, & Corkin, 2003; Uncapher, Hutchinson, & Wagner, 2011; Uncapher & Rugg, 2008, 2009; for a review see, Uncapher & Wagner, 2009).

Subsequent memory studies have also investigated the neural regions associated with the encoding of spatial information (Cansino, Maquet, Dolan, & Rugg, 2002; Park, Uncapher, & Rugg, 2008; Ross & Slotnick, 2008; Uncapher et al., 2006; Uncapher & Rugg, 2009; see also, Sommer et al., 2005; Sommer, Rose, Gläscher, Wolbers, & Büchel, 2005). During the encoding phase in these studies, participants were presented with items in different spatial locations. During the retrieval phase, old and new items were presented and participants classified each item as "old", and specified the previous spatial location, or "new". To isolate activity associated with spatial encoding, subsequent accurate item memory and

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accurate spatial location memory was contrasted with subsequent accurate item memory and inaccurate spatial location memory. These studies reported subsequent spatial memory activity in occipital cortex.

However, the previous studies did not report whether the effects in occipital cortex were spatially specific. This is of importance because numerous studies have shown that attention to items in a given visual field produces greater activity in the contralateral than the ipsilateral striate and extrastriate cortex (Heinze et al., 1994; Hopfinger, Buonocore, & Mangun, 2000; Kelley, Serences, Giesbrecht, & Yantis, 2008; Mangun, Hopfinger, Kussmaul, Fletcher, & Heinze, 1997; Martinez et al., 1999; Slotnick, Schwarzbach, & Yantis, 2003; Slotnick & Yantis, 2005; Tootell et al., 1998; Yantis et al., 2002; for a review see, Hopfinger, Woldorff, Fletcher, & Mangun, 2001). As such, if subsequent spatial memory and spatial attention are mediated, in part, by the same or similar neural mechanisms, subsequent spatial memory effects should produce contralateral effects in visual sensory regions.

In the current functional magnetic resonance imaging (fMRI) study, we evaluated whether subsequent spatial memory effects in visual sensory cortex were contralateral in an effort to assess the degree to which this cognitive process is mediated by spatial attention. During the encoding phase of the first experiment, participants were presented with abstract shapes to the left or right of fixation (see Figure 1). During the retrieval phase, old and new shapes were presented at fixation and participants classified each shape as old and previously on the left ("old-left"), old and previously on the right ("old-right"), or "new". Spatial encoding effects were identified by contrasting subsequently remembered item and spatial location information for a given visual field (i.e., encoding-left-hits and encoding-right-hits, which were assumed to have been attended) and subsequently forgotten item and spatial location information in the same visual field (i.e., encoding-left-misses and encoding-right-misses, which were assumed to have been unattended). To anticipate the results, contralateral subsequent memory effects were observed in extrastriate cortex. We also employed a novel individual-trial analysis to estimate the degree to which subsequently remembered items (encoding-hits) could be attributed to spatial processing or non-spatial processing.

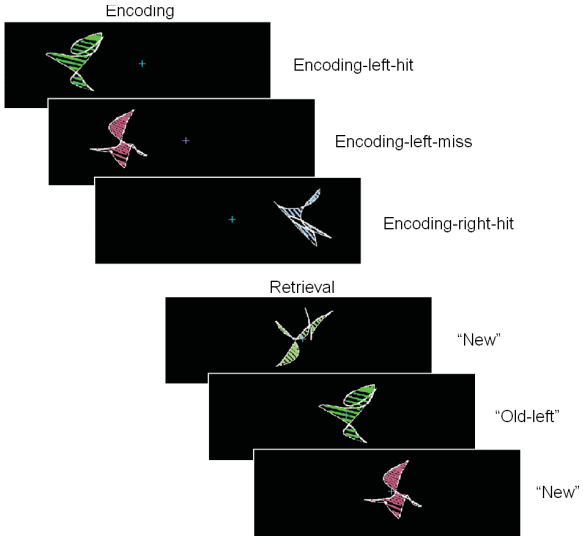

Figure 1. During encoding, abstract shapes with colored internal oriented lines were presented to the left or right of fixation. During retrieval, old and new shapes were presented at fixation. Participants classified each shape as previously presented in the left visual field ("old-left"), previously presented in the right visual field ("old-right"), or "new". Illustrative responses during retrieval are shown to the bottom right. Encoding trials were classified based on subsequent item memory and spatial location memory accuracy, as shown to the top right.

METHOD

Participants

Twelve right-handed participants (7 females, 18–35 years in age) with normal or corrected-to-normal visual acuity completed the study. The protocol was approved by the Massachusetts General Hospital Institutional Review board and informed consent was obtained from each participant.

Stimuli and Tasks

A total of 288 abstract shapes were used for the experiment, each outlined in white with colored oriented lines (see Figure 1; for shape construction details, see Slotnick & Schacter, 2004). Each participant completed six runs. During the encoding phase of each run, 32 abstract shapes were presented to the left or right of a central fixation cross (see Figure 1). Each shape subtended 5.5° of visual angle with the nearest edge 3° of visual angle from fixation and was presented for 2.5s every 3s. An equal number of shapes were presented in each visual field. While maintaining fixation, participants were instructed to remember each shape and its spatial location. During the retrieval phase of each run, the 32 previously presented (old) shapes from the encoding phase and 16 new shapes were presented at fixation for 2.5s every 4–12s. It is notable that there were twice as many old shapes, which may have biased participants to respond "old".

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This might be expected to increase the encoding-hit trial count due to guessing and thus reduce the significance of the corresponding effects; however, robust effects were observed such that bias was not of significant concern. Using a button box in their left hand, each participant classified shapes as old and previously presented in the left visual field ("old-left"), old and previously presented in the right visual field ("old-right"), or "new" (see Figure 1). Stimulus lists (old-left, old-right, and new) were counterbalanced across participants using a Latin Square design. No more than four shapes of a given type were shown sequentially, and shapes were never repeated across runs. Item memory accuracy, regardless of spatial location accuracy, was computed as p(old) x old-hit rate + p(new) x new-correct rejection rate (Macmillan & Creelman, 2005).

Data acquisition and analysis

Images were acquired on a 3 T Siemens Allegra scanner. Functional images were acquired using an echo-planar imaging sequence (TR = 2s, TE = 30ms, 30 slices, no gap, 4.5mm isotropic resolution). Anatomic images were acquired using a multiplanar rapidly acquired gradient-echo sequence (1.33 × 1 × 1mm resolution). Analysis was conducted using BrainVoyager QX. Functional data preprocessing included slice-time correction (the first slice was used as reference), motion correction (runs with greater than 3mm of motion were excluded), and temporal high pass filtering (i.e., removal of frequencies less than or equal to three cycles per run length). All volumes were normalized to Talairach space.

We first conducted a random effects general linear model analysis. For each participant, events were modeled based on stimulus onsets and the corresponding behavioral responses or, when no responses were given, the corresponding stimulus offsets. These models were then convolved with the default hemodynamic response function in BrainVoyager (i.e., two Gamma functions with a 5s onset of response, a 16s undershoot, a 1s dispersion, and a 6s response to undershot ratio). Across participants, voxels were classified as significant for a given contrast if the encoding-hit versus encoding-miss difference in beta-weights was significantly positive, using a one-tailed *t*-test at an individual voxel threshold of $p < .01$, and the encoding-hit beta-weight was significantly greater than zero. The latter constraint was imposed as classic spatial attention effects, which were hypothesized to mediate encoding-hits, are known to produce activation increases in contralateral visual sensory cortex. A cluster-extent threshold of 17 resampled voxels was enforced to correct for multiple comparisons to $p < .05$ (Slotnick, Moo, Segal, & Hart, 2003). This cluster extent was computed using a 10,000 iteration Monte Carlo simulation, which incorporated the contrast image spatial autocorrelation of 4.5mm (computed using custom software written in MATLAB).

To investigate whether the subsequent memory effects produced contralateral visual sensory effects, two contrasts were conducted: (1) encoding-left-hit > encoding-left-miss and (2) encoding-right-hit > encoding-right-miss. As mentioned previously, these contrasts mirror those employed to investigate contralateral spatial attention effects, as it can be assumed that a greater degree of attention was allocated during accurate encoding of spatial location (encoding-left-hits and encoding-right-hits) than was allocated during inaccurate encoding of spatial location (encoding-left-misses and encoding-right-misses, respectively). Group activity was projected onto a cortical surface representation of an individual participant (for precise anatomic locations, see Table 1; for surface reconstruction details, see Slotnick, 2005).

We also conducted a novel individual-trial modeling procedure. It is known that items can be encoded by spatial processes, such as spatial attention, but can also be encoded by non-spatial processes, such as verbal encoding. As such, the individual-trial analysis was conducted to estimate the proportion of encoding-hits that could be independently attributed to spatial processing and non-spatial processing. In short, for each participant, two models of encoding-hit activity were created, one that reflected spatial encoding alone and the other that reflected both spatial encoding and non-spatial encoding. As these models were nested, we could evaluate whether the addition of the non-spatial encoding process significantly improved the fit over the spatial encoding process alone. Moreover, this procedure allowed us to estimate the proportion of encoding-hit trials that could be attributed to spatial processing and non-spatial processing.

For each participant, event-related individual-trial activity associated with encoding-left-hits, encoding-left-misses, encoding-right-hits, and encoding-right-misses was extracted from the left and right extrastriate regions identified in the general linear model analysis. The number of trials per participant were 45.17 ± 3.15, 25.00 ± 2.09, 40.58 ± 3.60, and 30.67 ± 3.34, respectively (mean ± 1 standard error). Analysis was conducted based on the mean activity 4–8s after event onset, the expected maximum of the hemodynamic response (baseline corrected from –2 to 0s before stimulus onset). Then, encoding-hit histograms (corresponding to subsequently remembered item and

spatial location information) and encoding-miss histograms (corresponding to subsequently forgotten item and spatial location information) were generated for each participant based on the magnitudes of individual-trial activity within the contralateral extrastriate activations. In the first stage of the modeling procedure, each of these histograms was fit with a Gaussian model with parameters amplitude, mean, and standard deviation using the Marquardt least-squares algorithm (Press, Teukolsky, Vetterling, & Flannery, 1992; for a representative participant, see Figure 2A; the best-fit Gaussians to encoding-hit and encoding-miss activity are shown in red and blue, respectively). Of importance, the previous Gaussians modeled spatial encoding effects in extrastriate regions (see Figure 2A, red); however, as mentioned previously, some of the encoding-hit trials may have been mediated through non-spatial processes (e.g., verbal labels). To capture the degree to which non-spatial processes were engaged, the second stage of the modeling procedure entailed fitting two Gaussians to the encoding-hit histogram, one that reflected spatial processing (see Figure 2B, red) and one that reflected non-spatial processing (see Figure 2B, blue). The mean and standard deviation of the spatial encoding-hit Gaussian were fixed to the corresponding best-fit values obtained in the first stage of the model-fitting procedure. Similarly, the mean and standard deviation of the non-spatial Gaussian were fixed to the corresponding best-fit encoding-miss values from the first stage of the

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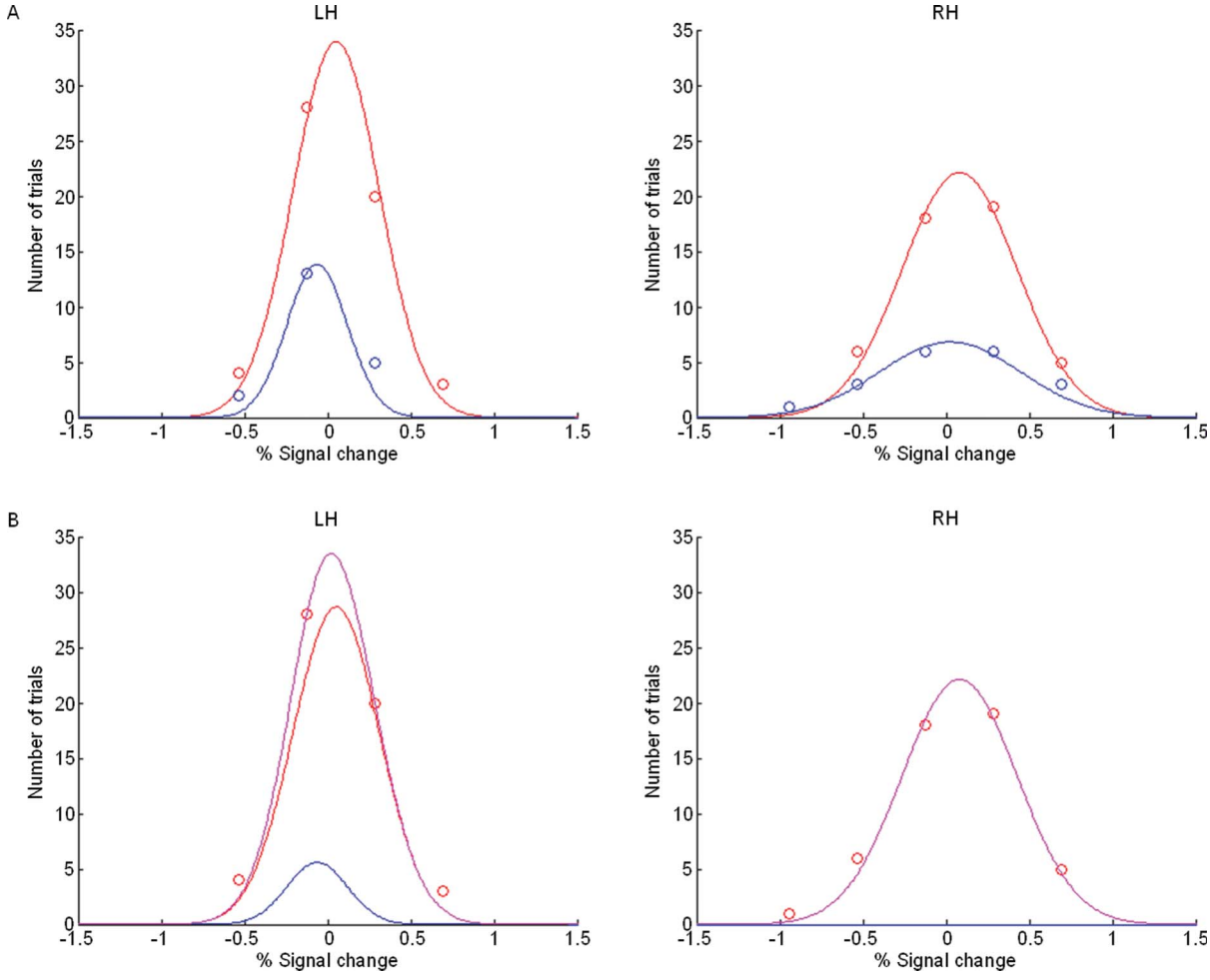

Figure 2. A. Representative participant's individual-trial event-related activity extracted from the contralateral extrastriate activations identified in the general linear model analysis. For each contralateral activation within the left hemisphere (LH) or the right hemisphere (RH), histograms of the encoding-hit magnitudes of activity (red circles) and the encoding-miss magnitudes of activity (blue circles) were each fit with a Gaussian model (best-fit models are shown in red and blue, respectively). B. The encoding-hit histogram was fit with two Gaussians, one reflecting spatial processing (in red) and the other reflecting non-spatial processing (in blue). The sum of these Gaussians (in magenta) was used to determine whether modeling non-spatial encoding significantly improved the fit over the single Gaussian alone, and was used to estimate the proportion of non-spatially encoded trials.

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model-fitting procedure, as non-spatial encoding would not be expected to produce contralateral extrastriate effects. In this way, only Gaussian amplitudes were free to vary in the second stage of the modeling procedure. The sum of the latter two Gaussians represented spatial processing and non-spatial processing associated with encoding-hits (see Figure 2B, magenta). These model fitting results were used in the following ways: (1) to compare the goodness-of-fit (chi-square) values to assess whether the addition of the non-spatial Gaussian (fit in the second stage of the modeling procedure) significantly improved the fit over the spatial Gaussian alone (fit in the first stage of the modeling procedure), which was possible given that these models are nested; and (2) to estimate the proportion of trials that corresponded to spatial processing and non-spatial processing.

RESULTS

Item memory accuracy was 67.2 ± 1.6% and, for items correctly classified as "old", spatial location accuracy was 70.0 ± 2.0% (mean ± 1 standard error; chance performance was 50%). As shown in Figure 3, the encoding-left-hit > encoding-left-miss contrast produced activity within the right extrastriate cortex (Brodmann area, BA 19), while the encoding-right-hit > encoding-right-miss contrast produced lateralized activity within the left extrastriate cortex (BA 18/19; Talairach coordinates are shown in Table 1). These contralateral subsequent memory effects mirror the known contralateral sensory effects that are considered a signature of spatial attention.

Figure 2A illustrates the encoding-hit and encoding-miss individual-trial histograms with the best-fit Gaussian model in each hemisphere of a representative participant (see Figure 2A, red and blue, respectively). Across participants, for the left hemisphere, the addition of the non-spatial Gaussian (see Figure 2B, left, in blue) significantly improved the fit over the single spatial Gaussian ($\chi^2(11) = 33.03$, $p < .001$; compare the magenta Gaussian in Figure 2B, left, with the red Gaussian in Figure 2A, left), and 20.65 ± 9.65% of encoding-hit trials could be attributed to non-spatial processing (see Figure 2B, left, blue). For the right hemisphere, the addition of the non-spatial processing Gaussian (see Figure 2B, right, in blue) did not significantly improve the fit over the spatial Gaussian alone ($\chi^2(11) = 2.29$, $p > .20$; the magenta Gaussian in Figure 2B, right, is identical to the red Gaussian in Figure 2A, right), thus all trials in the right hemisphere could be attributed to spatial processing. Based on the relative spatial and non-spatial Gaussian parameter values (see Figure 2B), 79.35% of trials in the left hemisphere and 100% of trials in the right hemisphere were mediated by spatial encoding.

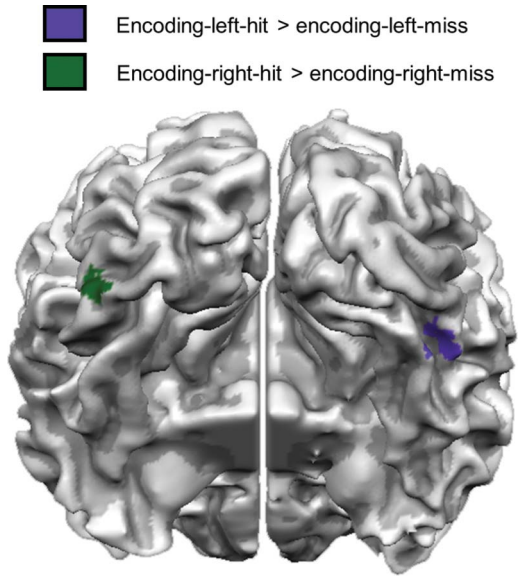

Figure 3. Extrastriate cortex activations produced by the encoding-left-hit > encoding-left-miss contrast and the encoding-right-hit > encoding-right-miss contrast are shown in purple and green, respectively (posterior-inferior view; key at the top).

TABLE 1
Neural regions associated with spatial encoding

Region	*BA*	*x*	*y*	*z*
Encoding-left-hit > encoding-left-miss				
Right extrastriate cortex	19	39	−60	−7
Encoding-right-hit > encoding-right-miss				
Left extrastriate cortex	18/19	−38	−69	0
Left intraparietal sulcus	7/40	−24	−68	30

Notes: BA refers to Brodmann area and coordinates (x, y, z) are in Talairach space.

GENERAL DISCUSSION

In the present study, the general linear model analysis revealed contralateral subsequent memory effects in extrastriate cortex that mirrored classic contralateral attention visual sensory effects. Considered in isolation, these parallel spatial encoding and spatial attention effects could be taken to suggest that the encoding of spatial information is mediated entirely by spatial attention. However, the individual-trial analysis revealed that accurate spatial encoding was mediated by spatial and non-spatial processing in the left hemisphere and was mediated by spatial processing alone in the right hemisphere.

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The present analyses were based on the assumption that encoding-misses were unattended during encoding. It could be argued that participants were attending, to some degree, to items that were subsequently forgotten. For instance, even if items were successfully attended during encoding, forgetting may have been due to a failure in the storage process or may have been due to a lack of access during retrieval. If participants had been attending to items that were subsequently forgotten to an appreciable degree, the activity associated with those events would have been positive in magnitude. The empirical results did not support this possibility, as the magnitude of encoding-miss activity was not significantly greater than 0 in either hemisphere ($t_{\text{right hemisphere}}(11) = 1.41$, $p > .05$; $t_{\text{left hemisphere}}(11) < 1.00$). This supports our assumption that encoding-misses were unattended during encoding.

The present results also depend on the assumption that the contralateral extrastriate encoding effects observed reflected spatial attention. While this assumption could be questioned, it is based on a wealth of evidence demonstrating that spatial attention modulates contralateral extrastriate cortex (Heinze et al., 1994; Hopfinger et al., 2000; Kelley et al., 2008; Mangun et al., 1997; Martinez et al., 1999; Slotnick et al., 2003; Slotnick & Yantis, 2005; Tootell et al., 1998; Yantis et al., 2002; for a review see, Hopfinger et al., 2001). Of relevance, a recent study that directly manipulated attention during encoding reported increased visual sensory activation for subsequently remembered versus forgotten items (Uncapher & Rugg, 2009; see also Uncapher et al., 2011). In that study, attentional modulation in the purported color processing region within visual sensory cortex was observed during the encoding of color information. These feature-based effects during encoding are similar to the feature-based effects that have been reported during attention to color (Chawla, Rees, & Friston, 1999; Liu, Slotnick, Serences, & Yantis, 2003). As such, this finding provides convergent evidence with the present results that successful encoding is mediated, to some degree, by attention. Still, it is important to underscore that this conclusion is based on the similarity between our contralateral subsequent memory effects and contralateral attention effects. One limitation of the present study is that we did not manipulate attention. Future work will need to address this limitation to more strongly link the processes of spatial encoding and spatial attention.

It is important to consider whether the present contralateral encoding effects might be attributable to eye-movements. According to an eye-movement account, the observed contralateral encoding effects could be produced by different fixation patterns between encoding-hits and encoding-misses. For instance, if participants maintained fixation during encoding-hit trials to a greater degree than during encoding-miss trials (i.e., gaze consistently shifted toward the stimuli during encoding-miss trials) this would have produced larger contralateral perception effects during encoding-hit trials due to greater peripheral stimulation. However, a relatively larger shift in gaze toward stimuli during encoding-miss trials would have produced a higher degree of accuracy for these items due to enhanced processing in the central visual field (see Velisavljević & Elder, 2008), while encoding-miss trials are by definition inaccurate. Moreover, an eye-movement account would predict similar contralateral encoding effects in the left and right hemispheres (as there is no reason to predict differences in fixation across visual fields), which is inconsistent with the differential individual-trial analysis results observed in the left and right hemispheres. Finally, although eye-movements were not monitored in the present paradigm, we monitored eye-movements in a very similar paradigm (involving peripherally presented abstract shapes during encoding) and participants maintained gaze to within 1° of central fixation (Slotnick & Thakral, 2011). Considered together, this evidence indicates that the current contralateral encoding effects are not attributable to eye-movements.

Previous lesion evidence indicates that the right hemisphere allocates attention to the left visual field and the right visual field while the left hemisphere allocates attention exclusively to the right visual field (Mangun et al., 1994; Mesulam, 1999). This relatively greater capacity of the right hemisphere in spatial attention processing was evidenced in the current results as all trials in the right hemisphere were found to be spatially encoded while a smaller proportion of trials in the left hemisphere were found to be spatially encoded. Furthermore, accuracy was significantly greater in the left visual field/the right hemisphere than in the right visual field/the left hemisphere, as measured by a higher number of encoding-hits ($t(11) = 2.24$, $p < .05$) and a lower number of encoding-misses ($t(11) = 3.14$, $p < .01$) in the left versus right visual field. These findings are consistent with the right hemisphere processing advantage associated with spatial attention.

More broadly, the hemispheric laterality revealed by the individual-trial analsis supports the categorical versus coordinate hemispheric visual-spatial processing asymmetry proposed by Kosslyn (1987). Specifically, the left hemisphere preferentially processes categorical information (e.g., the verbal representation "right of fixation"), while the right hemisphere preferentially processes precise coordinate information (e.g., the visual representation that an item is 3cm to the right

of fixation). Within this framework, the current hemispheric asymmetry could be due to the left hemisphere being more involved in non-spatial processing and the right hemisphere being more involved in spatial processing (see also, Slotnick, 2009; Slotnick, Moo, Tesoro, & Hart, 2001).

The present results suggest that spatial encoding is mediated, to a large degree, by spatial attention. This could be further tested using behavioral measures. For example, the present paradigm could be modified to include a probe during encoding, such as a briefly presented target immediately following each stimulus, either at the location of the stimulus or in the opposite hemifield. The present results would be bolstered if target accuracy at the location of the stimulus was greater than target accuracy in the opposite hemifield, which would mirror accuracy effects in behavioral attention paradigms. It should be highlighted that in this instance our fMRI results have been extended to make specific predictions regarding possible behavioral effects. This illustrates that fMRI results can be used to gain insight into the nature of cognitive processing, rather than simply mapping pre-established behavioral effects onto brain regions (a major criticism of fMRI).

To our knowledge, the present study is the first to provide evidence that spatial encoding effects mirror classic spatial attention effects in extrastriate cortex. Future work will be needed to extend the present findings by investigating the degree to which spatial attention mediates spatial encoding under different stimulus and task conditions.

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