

Hemifield-specific control of spatial attention and working memory: Evidence from hemifield crossover costs

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Attentional tracking and working memory tasks are often performed better when targets are divided evenly between the left and right visual hemifields, rather than contained within a single hemifield (Alvarez & Cavanagh, 2005; Delvenne, 2005). However, this bilateral field advantage does not provide conclusive evidence of hemifield-specific control of attention and working memory, because it can be explained solely from hemifield-limited spatial interference at early stages of visual processing. If control of attention and working memory is specific to each hemifield, maintaining target information should become more difficult as targets move between the two hemifields. Observers in the present study maintained targets that moved either within or between the left and right hemifields, using either attention (Experiment 1) or working memory (Experiment 2). Maintaining spatial information was more difficult when target items moved between the hemifields compared with when target items moved within their original hemifields, consistent with hemifield-specific control of spatial attention and working memory. However, this pattern was not found for maintaining identity information (e.g., color) in working memory (Experiment 3). Together, these results provide evidence that control of spatial attention and working memory is specific to each hemifield, and that hemifield-specific control is a unique signature of spatial processing.

Introduction

Research exploring the behavior of split-brain patients (i.e., patients with a severed corpus callosum) has famously highlighted functional asymmetries between the two cerebral hemispheres (e.g., a specialized role of the left hemisphere for speech; Kimura, 1973).

Importantly, split-brain patient research has also revealed the capability of the two cerebral hemispheres to function independently of one another. For example, split-brain patients complete visual search tasks more efficiently when processing demands are divided between the hemispheres during bilateral stimulus presentations (e.g., four items in the left visual hemifield, four items in the right visual hemifield), compared with when processing is restricted to one hemisphere during unilateral stimulus presentations (e.g., all eight items in the left visual hemifield; Luck, Hillyard, Mangun, & Gazzaniga, 1989, 1994). This bilateral field advantage is not found for healthy control participants performing the same search task (Luck et al., 1989, 1994), suggesting that the advantage occurs when the two cerebral hemispheres separately process information from each visual hemifield. Although such hemifield-specific processing initially seemed to be limited to split-brain patients, a bilateral field advantage has more recently been found for healthy observers across a variety of tasks (Alvarez & Cavanagh, 2005; Awh & Pashler, 2000; Delvenne, 2005; Delvenne, Castronovo, Demeyere, & Humphreys, 2011; McMains & Somers, 2004; Scaf et al., 2007; Umemoto, Drew, Ester, & Awh, 2010; for a review, see Delvenne, 2012), indicating that initially lateralized processing can influence behavior despite eventual integration by the corpus callosum. Unclear, however, is whether hemifield-specific processing in healthy individuals is restricted to early stages of visual processing, or instead extends to higher level processes such as attention and working memory.

If hemifield-specific processing is restricted to early stages of vision, attention and working memory may be limited by exclusively spatial interference. By this account, the bilateral field advantage occurs

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due to stronger interference between attended targets when they are in the same hemifield vs. when they are in separate hemifields, possibly because attention suppresses cortically neighboring representations (Franconeri, Alvarez, & Cavanagh, 2013; Scalf & Beck, 2010; Scalf, Torralbo, Tapia, & Beck, 2013; Störmer, Alvarez, & Cavanagh, 2014; Torralbo & Beck, 2008). Because information from each visual hemifield is initially routed separately to the cerebral hemispheres, items presented within a hemifield (unilaterally) are represented in closer proximity in early visual cortex than items presented in separate hemifields (bilaterally), even when the unilaterally and bilaterally presented items are the same physical and retinal distance from one another (Liu, Jiang, Sun, & He, 2009). For example, two items presented in different hemifields are represented in separate hemispheres in the primary visual cortex, whereas two items the same distance apart within a single hemifield are represented within the same hemisphere (Liu et al., 2009). On this account, the hemifield boundary serves as a buffer between representations in early stages of visual processing, resulting in less spatial interference between the representations of bilaterally presented items than between the representations of unilaterally presented items (Franconeri, Lin, Enns, Pylyshyn, & Fisher, 2008; Franconeri, Jonathan, & Scimeca, 2010; Liu et al., 2009; Scalf & Beck, 2010; Scalf, Torralbo, Tapia, & Beck, 2013; Störmer et al., 2014; Torralbo & Beck, 2008). The exclusively spatial interference account posits this hemifield-limited spatial interference is the sole cause of the bilateral field advantage (Franconeri et al., 2008; Franconeri et al., 2010), explaining the advantage without needing to consider the possibility of hemifield-specific control of attention and working memory.

Although hemifield-limited spatial interference alone could potentially account for the bilateral field advantage, some researchers have posited that separate control of attention and working memory exists for the left and right visual hemifields (Alvarez & Cavanagh, 2005; Chen, Howe, & Holcombe, 2013; Delvenne, 2005; Holcombe & Chen, 2012; Holcombe, Chen, & Howe, 2014; Umemoto et al., 2010), contributing to the bilateral field advantage as well. According to this account, bilaterally presented items may be processed by two separate high-level control systems (one control system for each hemifield), whereas the same targets presented unilaterally are processed less effectively by a single high-level control system (the control system responsible for the hemifield the targets are in). This hemifield-specific control account posits that information from each hemifield is processed separately until relatively late stages of visual processing. Although the bilateral field advantage found for attention (Alvarez & Cavanagh, 2005) and working memory (Delvenne, 2005) is consistent with this account, these

results are equally compatible with the exclusively spatial interference account, due to greater spatial interference between target representations during unilateral stimulus presentations than during bilateral stimulus presentations.

Because both the exclusively spatial interference and hemifield-specific control accounts are consistent with the bilateral field advantage, whether separate control of high-level processing exists for each hemifield remains unclear. Addressing this question is possible by testing whether healthy individuals have difficulty maintaining items that move between the hemifields. Such difficulty has previously been demonstrated by a patient without a splenium (the posterior portion of the corpus callosum; Noudoost, Afraz, Vaziri-Pashkam, & Esteky, 2006), presumably because of a failure of attentional control mechanisms for each hemifield to communicate. More recently, healthy individuals were also found to have difficulty tracking items that moved between hemifields (relative to items that moved within their original hemifields; Gill & Alvarez, 2010; Minami, Shinkai, & Nakauchi, 2019); however, these studies did not control for differences in spatial interference during between- vs. within-hemifield movements, making it unclear whether the between-hemifield cost occurred because of separate attentional control over each hemifield, or instead due to greater spatial interference during between-hemifield movements.

To test whether high-level control is specific to each hemifield in healthy individuals, observers in the present study performed either an attentional tracking (Experiment 1) or working memory (Experiments 2 and 3) task. In both types of tasks, target items were initially presented in diagonally opposite quadrants of the display (e.g., top-left and bottom-right). After a delay, the targets in the display shifted, moving either between the left and right visual hemifields or within their original hemifields. Critically, within- and between-hemifield trials were identical during the initial encoding of target information, ensuring that any performance differences were not due to differences in spatial interference during the initial encoding of target information (a possibility that cannot be ruled out by studies finding a bilateral field advantage). Additionally, differences in spatial interference during within- vs. between-hemifield movements were controlled for, ensuring that any performance differences were not due to spatial interference as targets moved within or between the hemifields (a possibility that was not ruled out by previous studies exploring between-hemifield costs). Therefore, if only early stages of visual processing are hemifield specific, observers should perform equally well when items move within vs. between hemifields. However, if high-level control of visual processing is specific to each hemifield, observers should perform worse when items move between the hemifields, a movement that would require

hemifield-specific control systems to exchange their information.

Experiment 1A: Multiple object tracking crossover

The magnitude of the bilateral field advantage in healthy observers varies across tasks (Delvenne, 2012), with the most extreme advantage occurring for multiple object tracking (Alvarez & Cavanagh, 2005), a task requiring observers to track a subset of moving items using attention (Cavanagh & Alvarez, 2005; Pylyshyn & Storm, 1988). Observers are able to track twice as many targets presented bilaterally compared with unilaterally (Alvarez & Cavanagh, 2005), a result that has been interpreted as separate control of attentional tracking in each hemifield (Alvarez & Cavanagh, 2005; Chen et al., 2013; Holcombe & Chen, 2012; Holcombe et al., 2014). However, this extreme bilateral field advantage can also be accounted for by a single attentional control system that has great difficulty tracking cortically nearby targets within a single hemifield, but little difficulty tracking cortically distant targets in separate hemifields (Franconeri et al., 2008; Franconeri et al., 2010; Störmer et al., 2014). To test whether hemifield-specific control occurs for attentional tracking, we created a tracking task where targets were presented bilaterally, before shifting either within their original hemifields or between the two hemifields. If separate attentional systems control tracking in each hemifield, then tracking should be more difficult when targets cross between hemifields, a movement that would require hemifield-specific attentional systems to exchange information. Although this result by itself would be insufficient for concluding the existence of hemifield-specific tracking mechanisms (due to the possibility of differential spatial interference between targets during between- vs. within-hemifield movements, which we examine in Experiment 1B), a between-hemifield crossover cost is a necessary initial result for making such a conclusion.

Methods

Participants

The procedures for all experiments described in this article were approved by Harvard University's Committee on the Use of Human Subjects. For each experiment, an anticipated effect size was determined using either the results of pilot data or a Monte Carlo simulation. A sample size providing at least 95% power to detect the anticipated effect size was then selected for each experiment (by entering the anticipated

effect size into G*Power 3.1; Faul, Erdfelder, Lang, & Buchner, 2009); because the anticipated effect size was determined separately for each experiment, each experiment has a unique sample size.

For Experiment 1A, 16 observers (9 female, $M_{\text{age}} = 22.6$) were recruited from the Harvard University Psychology Department study pool and participated after giving informed consent. This sample size was selected using the results of pilot data ($N = 16$, $d_z = 1.38$), and G*Power 3.1 (Faul et al., 2009), which indicated that 16 observers would be needed to achieve greater than 95% power to detect an effect size of $d_z = 1.00$ (Cohen, 1988).

Stimuli

Stimuli consisted of black (luminance = 1.89 cd/m^2) dots presented in each quadrant of a gray (19.5 cd/m^2) square background (1200×1200 pixels), which was centered on the screen (1920×1200 pixels, refresh rate = 60 Hz, viewing distance = 56 cm). The midpoints of each of the four dot pairs were located 90° apart along an imaginary circle of radius 11.8° with an origin at the center of the screen; in each quadrant, the midpoint of the dot pair was an equal distance from the horizontal and vertical midlines. Each dot had a diameter of 1° , and the distance between the centers of each dot within a pair was 5.2° . A white (127 cd/m^2) fixation cross of diameter 0.8° was presented at the center of the screen.

Procedure

Figure 1 depicts the experimental design. At the beginning of each trial, a pair of black dots was presented in each quadrant of a gray square background (eight dots total). Two dots in diagonally opposite quadrants were cued as targets (e.g., one dot in the top-left quadrant, and one dot in the bottom-right quadrant) by flashing gray with a black border (3 cycles, 1 Hz). The target dots gradually faded from gray to black (for 1000 ms) as the dot pairs begin rotating within each quadrant, randomly changing spin direction (changes of spin direction were independent for each dot pair). After rotating in place for 3,000 ms, all four dot pairs shifted 90° along an imaginary circle of radius 11.8° (either all clockwise or counterclockwise) while continuing to spin, resulting in each pair moving to a new quadrant of the screen. This shift to a new location on the screen took 433 ms (26 frames of movement with a 60 Hz monitor). Each dot pair was always oriented parallel to the midline it was crossing at the moment of crossing into a new quadrant (e.g., dot pairs moving horizontally between hemifields were always oriented vertically as they crossed the vertical midline; see Figure 1, third panel); this positioning prevented two targets from being within the same hemifield during between-hemifield positioning (besides

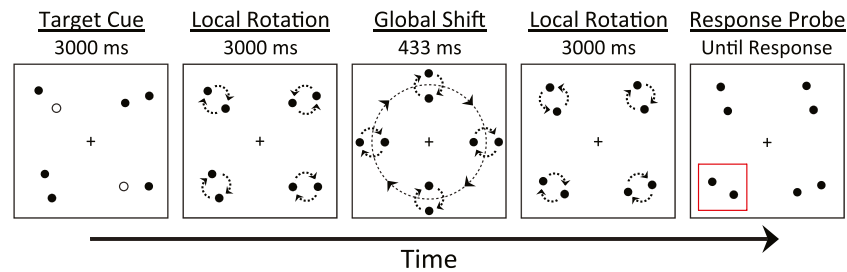


Figure 1. Design of [Experiment 1](#). Target dots in diagonally opposite quadrants were cued before fading to black. Dot pairs rotated locally for 3,000 ms before undergoing a global shift. During the global shift, all dot pairs moved along an imaginary circle either clockwise or counterclockwise (motion path represented by dashed circle in third panel, where dots are depicted halfway through the global shift). During the global shift, dot pairs moved 45° along the imaginary circle (the moment of the global shift depicted in third panel) before either continuing for another 45° in the same direction to a new location ([Experiment 1A](#) and [Experiment 1B](#) cross trials), or shifting 45° in the opposite direction back to their original locations ([Experiment 1B](#) return trials). After reaching their final locations, dot pairs rotated in place for another 3,000 ms before one of the two pairs containing a target was probed for response. A clockwise shift to a new location (between-hemifield) is depicted here. See online Supplementary Movies S1 and S2 for Movie demonstrations.

one frame where the midpoint of all dots were on either the vertical or horizontal midline). Because target dots were always presented in diagonally opposite quadrants, the shifting of the dot pairs resulted in both target dots moving either vertically within the same hemifield (within-hemifield movement), or horizontally between the hemifields (between-hemifield movement). Once the dot pairs reached their new locations, they continued to spin in place while randomly changing direction for another 3,000 ms before coming to a stop. Once the dots came to a stop, one of the two pairs containing a tracked target was probed for response by marking the pair's quadrant with a red (36.0 cd/m²) border. At this point, observers indicated which dot in the probed pair was the tracked target using a mouse click (a two-alternative forced choice, making chance performance 50%). Observers were given feedback after each trial, with the selected dot turning green (76.6 cd/m²) when observers were correct, and red (36.0 cd/m²) when they were incorrect.

Observers were instructed to keep central fixation during all trials (which was monitored via an eye-tracking device; EyeLink 1000, SR Research, Ottawa, ON, Canada), but told that they could blink if necessary. Trials were terminated if observers broke fixation during tracking (>2° from fixation) for 250 ms, which permitted observers to blink but not to hold their gaze away from fixation. Terminated trials were moved to the end of the experiment, where they were presented with unique trajectories (preventing observers from strategically breaking fixation to gain information about target movements). For both [Experiment 1A](#) and [1B](#), analyses of eye-tracking data revealed no statistically significant differences in distance from fixation, horizontal eye position, or vertical eye position for within- vs. between-hemifield trials

(Supplementary Material, Appendix A1). Additionally, individual differences in deviation from fixation were not associated with accuracy differences for within- vs. between-hemifield trials.

After completing eight practice trials (four within-hemifield and four between-hemifield trials randomly intermixed), observers completed four blocks of 24 trials each (96 trials total, 48 within-hemifield and 48 between-hemifield trials randomly intermixed). Before the main experimental trials, a thresholding session (32 trials) was conducted (using the Bayesian QUEST procedure; [Watson & Pelli, 1983](#)) to determine the rotational speed at which each participant could track two rotating dots with 85% accuracy when the dot pairs remained in their original quadrants throughout the trial. The parameters of the thresholding session were identical to the main experimental trials, except that the dot pairs did not shift to a new location, instead rotating in place for 6000 ms. Each observer's individual threshold speed (in degrees of rotation per second; $M = 371.7$ deg/s, $SD = 142.8$ deg/s) was used during the main experimental trials. Observers completed eight practice trials before beginning the 32-trial thresholding session.

Results

Observers were better at identifying target dots following within-hemifield movements ($M = 77.2\%$, $SD = 12.1\%$) than following between-hemifield movements ($M = 66.7\%$, $SD = 13.4\%$; $t(15) = 3.95$, $p = .001$, $d_z = 0.99$; see [Figure 2A](#)). This result is consistent with hemifield-specific control systems for attentional tracking, which must exchange information during between-hemifield movements.

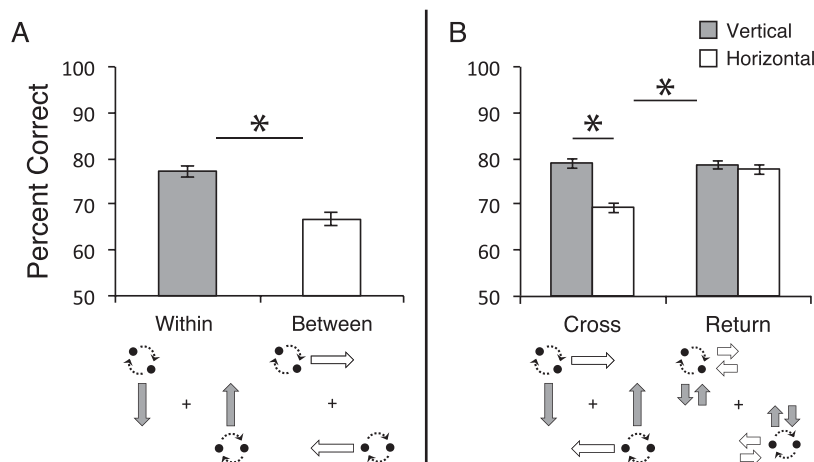


Figure 2. Results of [Experiments 1A](#) and [1B](#). Error bars represent within-subject *SEM* ([Cousineau, 2005](#)). (A) Observers were significantly better at tracking targets that shifted vertically within their original hemifields than targets that shifted horizontally between the hemifields. (B) Replicating [Experiment 1A](#), observers were significantly better at tracking targets that shifted vertically within their original hemifields than targets that shifted horizontally between the hemifields (cross conditions). However, there was no difference in tracking performance for targets that shifted vertically (to the horizontal midline) or horizontally (to the vertical midline) before returning to their original locations (return conditions). Note that irrelevant dot pairs were presented in the nontarget quadrants (see [Figure 1](#)), but are not depicted here for clarity.

Experiment 1B: Control for potential midline effects

Although the between-hemifield cost found in [Experiment 1A](#) is consistent with hemifield-specific attentional control, this result could also be explained by a single attentional control system having difficulty representing targets at the vertical midline between hemifields, an area that may be represented by both cerebral hemispheres ([Fendrich, Wessinger, & Gazzaniga, 1996](#)). Because of this representational overlap, attending to targets at the vertical midline between the left and right visual fields may be more challenging than attending to targets at the horizontal midline between the upper and lower visual fields ([MacKeben, 1999](#)), which would explain the between-hemifield cost in [Experiment 1A](#) without needing to appeal to hemifield-specific attentional control. To test whether difficulty attending to information at the vertical midline explains the between-hemifield crossover cost, we replicated the conditions from [Experiment 1A](#), and added two new return conditions ([Figure 2B](#)), where targets moved to the vertical or horizontal midline, but rather than continuing to move to new locations, instead returned to their original locations. Time spent at the vertical or horizontal midline was equivalent both when items moved to the midline and continued to new locations (cross conditions) and when items moved to the midline before returning to their original locations (return conditions). Therefore, if the between-hemifield

crossover cost in [Experiment 1A](#) was due to difficulty tracking at the vertical midline, then observers should perform worse for horizontal shifts than for vertical shifts for both the cross and return conditions. However, if the between-hemifield crossover cost is a consequence of hemifield-specific attentional control, then observers should perform worse for horizontal shifts than for vertical shifts only for the cross conditions, and not for the return conditions (where the targets remained within their original hemifields).

Methods

Participants

Forty observers (32 female, $M_{\text{age}} = 20.2$) were recruited from the Harvard University Psychology Department study pool and participated after giving informed consent. This sample size was selected using the results of pilot data ($N = 13$, interaction $d_z = 0.69$), and G*Power ([Faul et al., 2009](#)), which indicated that 40 observers would result in greater than 95% power to detect an interaction effect of $d_z = 0.60$.

Stimuli

The stimuli were the same as those used in [Experiment 1A](#).

Procedure

In addition to completing the same thresholding procedure to select rotational speed ($M = 403.8$ deg/s, $SD = 140.4$ deg/s) and the two experimental conditions described in [Experiment 1A](#) (cross conditions), observers completed two new conditions where targets returned to their original locations after reaching the vertical or horizontal midline (third panel of [Figure 1](#)), rather than continuing to new locations (return conditions). The time spent at the midline and trial duration was equivalent for all experimental conditions; the only differences between conditions were (A) whether the targets shifted horizontally or vertically, and (B) whether the targets continued to new locations after reaching the midline (cross conditions), or instead returned to their original locations (return conditions). Observers completed eight alternating blocks of cross and return trials, with each block containing 24 trials (with horizontal and vertical trials randomly intermixed within each block). Whether the first block contained cross or return trials was counterbalanced between observers.

Results

A 2 (movement direction: horizontal vs. vertical) \times 2 (trial type: cross vs. return) repeated-measures analysis of variance (ANOVA) revealed a significant movement direction \times trial type interaction ($F(1, 39) = 14.67$, $p < 0.001$, $d_z = 0.61$), as well as significant main effects of movement direction ($F(1, 39) = 27.13$, $p < 0.001$) and trial type ($F(1, 39) = 9.70$, $p = .003$). Replicating [Experiment 1A](#), when items moved to a new location, observers were better at identifying target dots after vertical shifts within hemifields ($M = 78.8\%$, $SD = 11.1\%$) than after horizontal shifts between hemifields ($M = 69.2\%$, $SD = 10.2\%$; $t(39) = 6.28$, $p < 0.001$, $d_z = 0.99$; see [Figure 2B](#)). When items returned to their original locations, however, there was no significant difference in tracking performance for horizontal ($M = 78.4\%$, $SD = 10.4\%$) vs. vertical shifts ($M = 77.4\%$, $SD = 10.3\%$; $t(39) = 0.66$, $p = .52$, $d_z = 0.10$).

Discussion: Experiments 1A and 1B

[Experiment 1A](#) revealed a cost for attentively tracking targets that move between the hemifields, and [Experiment 1B](#) demonstrated that this cost was not due to either difficulty tracking at the border between hemifields or differences in spatial interference for within- vs. between-hemifield movements. These results provide evidence for hemifield-specific control of attentional tracking, because a single attentional

control system cannot account for a crossover cost that occurs despite controlling for potential differences in spatial interference at the vertical and horizontal midlines of the visual field. Instead, these results are consistent with hemifield-specific control systems for attentional tracking, which are able to successfully track targets that remain within their original hemifields, but have difficulty exchanging information when targets simultaneously cross between hemifields.

Notably, [Experiment 1B](#) used a blocked design to separate cross trials (where targets moved to a new quadrant) and return trials (where targets moved to the horizontal or vertical midline before returning to their original quadrant), rather than randomly intermixing these two trial types in a nonblocked design. Because the representation of information near the hemifield border is influenced by observers' expectations about whether targets will move between hemifields ([Drew, Mance, Horowitz, Wolfe, & Vogel, 2014](#)), it is possible that the results of [Experiment 1B](#) would have differed with a nonblocked design. Specifically, accuracy for horizontal cross and horizontal return trials may have been worse with a nonblocked design, as uncertainty about whether or not targets would cross between hemifields may have caused hemifield-specific attentional control systems to inefficiently exchange their information as targets moved toward the hemifield border, consistent with the findings of previous neurophysiological work ([Drew et al., 2014](#)). Although testing the influence of observers' expectations on hemifield crossover costs is important for better understanding hemifield-specific attentional control, using a blocked design in [Experiment 1B](#) allowed the predictions of hemifield-specific attentional control and exclusively spatial interference to be compared, as a Trial type \times Movement direction interaction is predicted only by hemifield-specific attentional control, whereas the lack of this interaction is predicted by exclusively spatial interference. With a nonblocked design, the lack of a significant interaction is compatible with both hemifield-specific control and exclusively spatial interference, because both accounts would predict greater difficulty for the horizontal return condition than for the vertical return condition; hemifield-specific control could explain this difference as a consequence of hemifield-specific attentional control systems exchanging their information as targets approach the vertical midline (due to uncertainty over whether targets might cross hemifields), whereas exclusively spatial interference could explain this difference as a general difficulty of tracking at the vertical midline. Thus, in [Experiment 1B](#) a blocked design was the better approach for addressing whether the results of [Experiment 1A](#) were due to hemifield-specific attentional control.

Experiment 2A: Spatial working memory crossover

Multiple object tracking tasks require observers to monitor the positions of target items, requiring attentive filtering of continuous perceptual input (Cavanagh & Alvarez, 2005; Pylyshyn & Storm, 1988). Working memory tasks, in contrast, require representations to be maintained over time in the absence of the original perceptual input (Baddeley & Hitch, 1974). Although performance on both types of tasks is positively correlated with measures of fluid intelligence (Engle, Laughlin, Tuholski, & Conway, 1999; Oksama & Hyönä, 2004), attentional tracking and working memory rely on partially distinct mechanisms, as evident from incomplete dual task interference between tracking and working memory tasks (Fougnie & Marois, 2006), partially distinct electrophysiological responses while completing perceptually matched tracking and working memory tasks (Drew, Horowitz, Wolfe, & Vogel, 2011), the failure of training benefits to generalize between attentional tracking and working memory tasks (Arend & Zimmer, 2012; Thompson et al., 2013), the selective impairment of multiple object tracking (but not spatial working memory) after administration of psilocybin (a serotonin agonist; Carter et al., 2005), and greater developmental abnormalities for spatial tracking than for spatial working memory in individuals with Williams syndrome (O'Hearn, Hoffman, & Landau, 2010).

Although this evidence suggests that attentional tracking and working memory are at least partially distinct, there also seems to be a strong relationship between them. For instance, attentive tracking and working memory have strong correlations in performance (Oksama & Hyönä, 2004), high dual task interference (Lapierre, Cropper, & Howe, 2017), and similar neural signatures (Drew et al., 2011; Drew & Vogel, 2008; Vogel & Machizawa, 2004). These findings suggest that, although attentional tracking and working memory are partially distinct, the two processes likely share common components.

Noting the similarities between attentional tracking and working memory, previous research has explored whether the bilateral field advantage found for attentional tracking also exists for working memory. Although not as extreme as the advantage for attentional tracking (perhaps due to greater demands of spatial updating with multiple object tracking; Drew et al., 2011), a bilateral field advantage was found for spatial working memory (Delvenne, 2005), suggesting the possibility of hemifield-specific maintenance of information in spatial working memory. However, because spatial interference, which impacts working memory performance (Ahmad et al., 2017), is greater

between the representations of items presented within the same hemifield than between the representations of items presented in separate hemifields (Franconeri et al., 2010; Liu et al., 2009; Störmer et al., 2014), whether this finding reflects hemifield-specific control of spatial working memory remains unclear. Instead, the bilateral field advantage for spatial working memory may result from greater interference between encoded items during unilateral presentations than during bilateral presentations. To explore the possibility of hemifield-specific control of spatial working memory, observers in Experiment 2A completed a spatial working memory task where displays were always encoded bilaterally, before shifting either within or between the hemifields during maintenance (paralleling Experiment 1A).

Methods

Participants

Sixty observers (31 male, $M_{\text{age}} = 36.2$) were recruited via Amazon Mechanical Turk and participated after giving informed consent. This sample size was selected using the results of pilot data ($N = 97$, $d_z = 0.56$), and G*Power (Faul et al., 2009), which indicated that 60 observers would result in greater than 95% power to detect an effect of $d_z = 0.50$.

Stimuli

At the beginning of the experiment, a white square with a red border (650×650 pixels) was presented on the screen. Observers were instructed to adjust the zoom percentage of their browser to make this square as large as possible while still remaining visible—the experiment did not proceed unless the entire square was visible. Stimuli were black 2×2 grids (150×150 pixels) whose midpoints were presented at diagonally opposite corners of an invisible square (length = 325 pixels) centered on the screen. Black dots (40 pixels) were presented within two cells of each grid at the beginning of each trial, and a single black dot probe was presented within one cell of one grid at the end of each trial. A black fixation cross (width = 22 pixels) was presented at the center of the screen.

Procedure

Observers were instructed to keep their eyes on the fixation cross at all times while completing trials. At the beginning of each trial, two 2×2 grids appeared at diagonally opposite corners (e.g., top-left and bottom-right) of the screen (see Figure 3). After a 500-ms delay, black dots appeared in two of the four cells of each grid. Both grids never contained the same arrangement

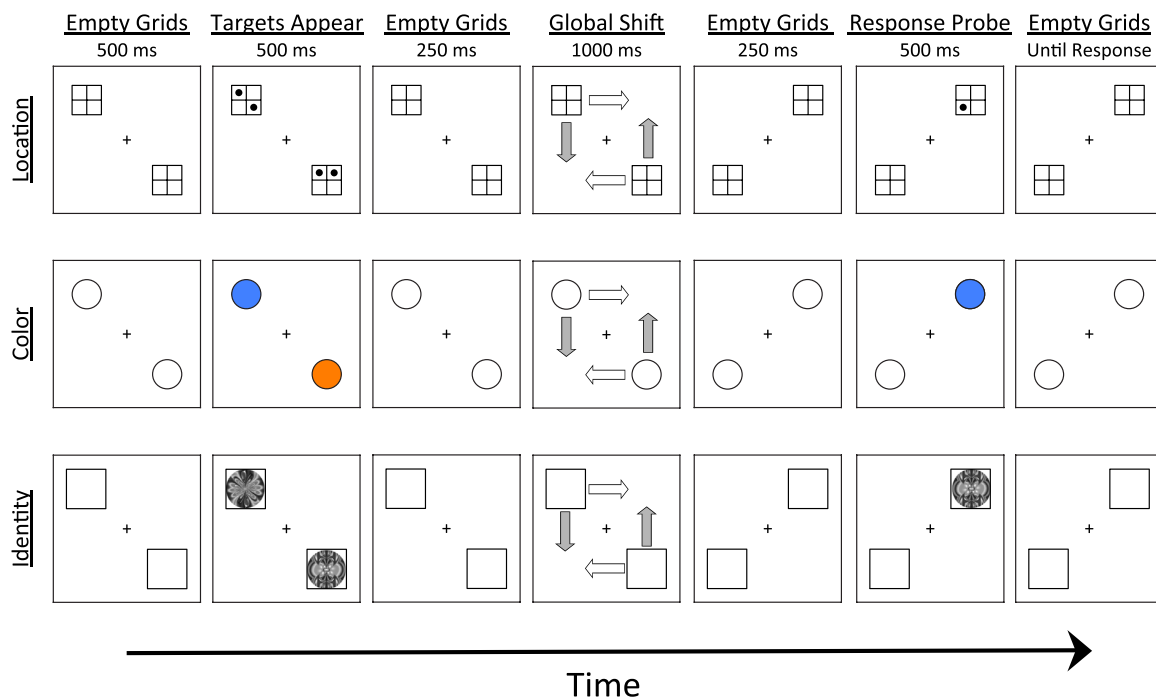


Figure 3. Design of Experiments 2 and 3. Figure contains a separate row for working memory location trials (Experiments 2A to 3D), color trials (Experiments 3A and 3B), and identity trials (Experiments 3C and 3D). After targets were displayed for 500 ms, items shifted either within (gray arrows) or between (white arrows) the hemifields. Return trials in Experiment 2B were similar to the location trials depicted here, except for the empty grids returned to their original position after reaching the horizontal or vertical midline (rather than continuing to a new location). See online Supplementary Movies S3 through S6 for Movie demonstrations.

of dots on a single trial (e.g., dots never appeared in the top-left and top-right cells of both grids), although dots could appear within a single location in both grids (e.g., dots might appear in the top-left and top-right cells of one grid, and the top-left and bottom-left cells of the other). After being presented for 500 ms, the dots were removed from the grids. The empty grids remained in their original locations for 250 ms, before both shifting either vertically or horizontally to adjacent quadrants of the screen, a movement that lasted 1000 ms. Once the grids reached their final locations, they remained empty for 250 ms, after which a cell in one grid was probed by being filled with a dot for 500 ms. Observers used a keypress to indicate whether the probed cell had previously contained a dot (pressing “s” if it had, or “d” if it had not). This two-alternative forced-choice response resulted in chance performance being 50%.

Observers completed 64 trials (32 within-hemifield trials and 32 between-hemifield trials randomly intermixed), receiving accuracy feedback after each response. Before completing the main experimental trials, observers completed 16 practice trials that were identical to the main experimental trials, except that the empty grids remained in their original quadrants instead of moving to new locations. Although verbal rehearsal strategies do not typically improve

working memory capacity (Oberauer, 2019) and would have influenced within and between-hemifield trials equally, observers were nonetheless asked to avoid verbal rehearsal strategies using the following instructions: “We are specifically interested in studying visual memory, so please DO NOT use any verbal strategies to complete the task. If you find yourself using verbal strategies (such as talking to yourself or saying words in your head), try repeating a simple word (like “the”) to yourself in your head.”

Results

Observers were more accurate reporting whether the probed cell had previously contained a dot following within-hemifield movements ($M = 85.2\%$, $SD = 14.6\%$) than following between-hemifield movements ($M = 78.6\%$, $SD = 14.0\%$; $t(59) = 6.18$, $p < .001$, $d_z = .80$; see Figure 4A). This result is consistent with hemifield-specific maintenance of spatial information in working memory. A post hoc analysis indicated that this result was not a consequence of greater mirror image confusion when items moved between the hemifields vs. within their original hemifields (Supplementary Material, Appendix A2).

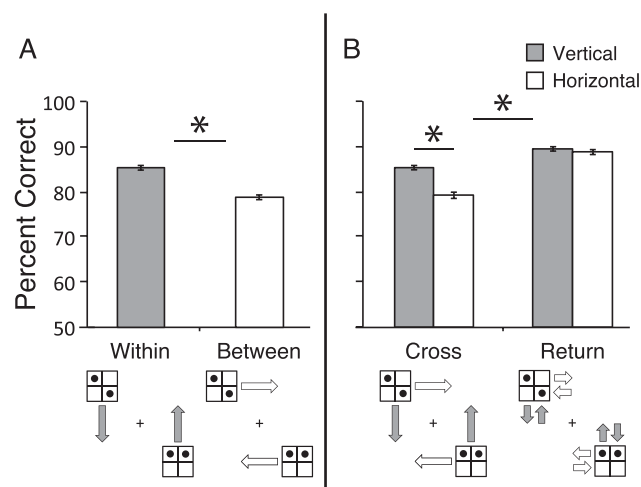


Figure 4. Results of [Experiments 2A and 2B](#). Error bars represent within-subject *SEM* ([Cousineau, 2005](#)). (A) Observers were significantly better at remembering dot locations when grids moved vertically within their original hemifields than when grids moved horizontally between the hemifields. (B) In addition to replicating [Experiment 2A](#) (cross conditions), no difference in working memory performance was found between grids that shifted vertically (to the horizontal midline) and grids that shifted horizontally (to the vertical midline) before returning to their original locations (return conditions).

Experiment 2B: Control for potential midline effects

Similar to [Experiment 1A](#), the results of [Experiment 2A](#) could potentially be explained by difficulty performing the task as items passed over the vertical midline (during between-hemifield movements), an area of representational overlap ([Fendrich et al., 1996](#)) where focusing attention may be difficult ([MacKeben, 1999](#)). Although the remembered dots were not present as the empty grids moved to the midline during [Experiment 2A](#), a decreased ability to maintain the dots' locations in working memory could have possibly occurred while the grids were on the vertical midline. To test this possibility, [Experiment 2B](#) compared working memory performance in the conditions from [Experiment 2A](#) (cross conditions) to two new return conditions (see [Figure 4B](#)), where the midpoints of the empty grids moved to the vertical or horizontal midline, but rather than continuing to move to new locations, instead returned to their original locations (paralleling [Experiment 1B](#)). If the between-hemifield crossover cost in [Experiment 2A](#) was due to difficulty maintaining target information at the hemifield boundary, then observers should perform worse for horizontal shifts than vertical shifts for both the cross and return conditions. However, if the

between-hemifield crossover cost in [Experiment 2A](#) is a consequence of hemifield-specific maintenance of information in spatial working memory, then observers should perform worse for horizontal shifts than for vertical shifts only for the cross conditions, but not for the return conditions.

Methods

Participants

One hundred observers (54 male, $M_{\text{age}} = 34.4$) were recruited via Amazon Mechanical Turk and participated after giving informed consent. This sample size was selected using the results of pilot data ($N = 100$, interaction $d_z = 0.63$), and G*Power ([Faul et al., 2009](#)), which indicated that 100 observers would result in greater than 95% power to detect an interaction effect size of $d_z = 0.40$.

Stimuli

The stimuli in [Experiment 2B](#) were the same as those used in [Experiment 2A](#).

Procedure

In addition to completing the same practice trials and two experimental “cross” conditions described in [Experiment 2A](#), observers completed two new “return” conditions, where the empty grids returned to their original locations after their midpoints reached the vertical or horizontal midline, rather than continuing to a new location. The time spent at the midline and trial duration was equivalent for all experimental conditions; the only differences between conditions were (A) whether the grids shifted horizontally or vertically, and (B) whether the grids continued to new locations after reaching the midline (cross conditions), or instead returned to their original locations (return conditions). Observers completed one block of cross trials (64 total trials, 32 vertical trials and 32 horizontal trials randomly intermixed) and one block of return trials (64 total trials, 32 vertical trials and 32 horizontal trials randomly intermixed), the order of which was counterbalanced between observers. Observers were asked to avoid using verbal rehearsal strategies using the same instructions as [Experiment 2A](#).

Results

A 2 (movement direction: horizontal vs. vertical) \times 2 (trial type: cross vs. return) repeated-measures ANOVA revealed a significant Movement direction \times Trial type interaction ($F(1, 99) = 22.60$, $p < 0.001$,

$d_z = 0.48$; see [Figure 4B](#)), as well as significant main effects of movement direction ($F(1, 99) = 34.64$, $p < 0.001$) and trial type ($F(1, 99) = 73.12$, $p < 0.001$). Replicating [Experiment 2A](#), when the grids moved to a new location, observers were better at identifying target dots following vertical shifts within-hemifield ($M = 85.2\%$, $SD = 14.9\%$) than following horizontal shifts between-hemifield ($M = 79.1\%$, $SD = 14.1\%$; $t(99) = 6.66$, $p < 0.001$, $d_z = 0.67$). When items returned to their original locations, however, there was no significant difference in tracking performance for vertical ($M = 89.3\%$, $SD = 13.0\%$) vs. horizontal shifts ($M = 88.7\%$, $SD = 14.1\%$; $t(99) = 1.00$, $p = .32$, $d_z = 0.10$).

Discussion: Experiments 2A and 2B

The between-hemifield crossover cost for the working memory task in [Experiment 2A](#) provides evidence for hemifield-specific control of spatial working memory. Importantly, within- and between-hemifield trials were identical during the encoding of target locations, indicating that the between-hemifield cost resulted from hemifield-specific maintenance of spatial information. Additionally, [Experiment 2B](#) ruled out difficulty maintaining information at the vertical midline as the cause of the hemifield-crossover cost, because observers displayed no cost for remembering displays that moved to the vertical midline before returning to their original locations. Together, these results are consistent with hemifield-specific maintenance of spatial information in working memory and cannot be accounted for by a single control system limited by spatial interference.

Previous research has documented behavioral ([Lapierre et al., 2017](#); [Oksama & Hyönä, 2004](#)) and neural evidence ([Drew et al., 2011](#); [Drew & Vogel, 2008](#); [Vogel & Machizawa, 2004](#)) that attentional tracking and working memory rely on overlapping cognitive mechanisms. The finding of a between-hemifield crossover cost for both attentional tracking ([Experiments 1A and 1B](#)) and spatial working memory ([Experiments 2A and 2B](#)) suggests that one of these shared mechanisms is hemifield-specific control of represented information. Importantly, the present results indicate that this shared lateralized component is not restricted to the initial encoding of information—displays were identical for within- and between-hemifield movements during the initial encoding of information—and differed only in whether information moved between or within the hemifields as information was maintained with attention or working memory. [Experiments 3A and 3B](#) address whether this hemifield-specific control is specific to spatial information, or additionally occurs for identity information (e.g., color).

Although eye position was not monitored in [Experiments 2A and 2B](#), failing to maintain central fixation would be more likely to diminish the observed effect (a between-hemifield cost for maintaining spatial information in working memory) than to artificially produce it. Failing to maintain central fixation would prevent displays from being presented to separate hemifields, making the two experimental conditions in [Experiment 2A](#) more similar to one another by removing the possibility of a between-hemifield movement (i.e., even when moving between the left and right sides of the screen, the displays would not be moving between the left and right visual fields if observers failed to keep central fixation). Therefore, the observed effect of a between-hemifield crossover cost may have been even more pronounced if central fixation had been enforced with an eye tracker. Although we cannot rule out the possibility that the interaction observed in [Experiment 2B](#) was due to observers maintaining central fixation during cross trials but not during return trials, we have no reason to suspect that observers would systematically adopt such a strategy.

Experiment 3A: Spatial vs. color working memory

Previous work has shown that a bilateral field advantage occurs when tasks require spatial attention or working memory, but not when they require feature-based attention ([Alvarez, Gill, & Cavanagh, 2012](#)) or working memory ([Delvenne, 2005](#); [Holt & Delvenne, 2014](#); [Umemoto et al., 2010](#)). This dissociation may arise because spatial information is maintained by lateralized, hemifield-specific control systems, whereas identity features (such as color) are maintained by nonlateralized, global control systems. This possibility is consistent with nonspatial tasks relying more on interactions between the cerebral hemispheres than spatial tasks (which rely primarily on within-hemisphere interactions; [Cohen & Maunsell, 2011](#); [Mishkin, & Ungerleider, 1982](#)), as well as feature-based attention spreading globally throughout the entire visual field ([Saenz, Buracàs, & Boynton, 2003](#); [Störmer and Alvarez, 2014](#)). In the present study, we test whether a dissociation occurs for maintaining spatial information (relative location) vs. identity information (color) in working memory as items move between the hemifields. If the previously observed differences in spatial vs. feature-based attention and working memory are a result of lateralized control being specific to spatial information, then a hemifield crossover cost is expected for spatial working memory, but not color working memory.

Methods

Participants

One hundred observers ($M_{\text{age}} = 33.7$, 56 male) were recruited via Amazon Mechanical Turk and participated after giving informed consent. This sample size was selected using the results of a Monte Carlo simulation (which assumed no difference for within- and between-hemifield performance for the color working memory task) and G*Power (Faul et al., 2009), which indicated that 100 observers would result in greater than 95% power to detect an interaction effect of $d_z = 0.40$.

Stimuli

The stimuli for the spatial working memory task were the same as those used in Experiments 2A and 2B. For the color working memory task, stimuli were two circles (155×155 pixels) instead of grids, which were each filled with a different color 180° away in CIELAB color space; all other aspects of the display were the same as the spatial working memory task described in Experiment 1A.

Procedure

In addition to again completing the two experimental conditions described in Experiment 2A for the spatial working memory task, observers completed two new color conditions (Figure 3) requiring them to remember the color of a circle presented in each hemifield. After the circle colors were briefly presented (same timing parameters as the spatial working memory task described in Experiment 2A, only with circle colors instead of dot locations), each circle turned white before shifting either vertically within the same hemifield or horizontally between hemifields. After reaching their final locations, one circle was probed by being filled with color (either the circle's original color, or a different color 45° away in CIELAB color space). Observers used a keyboard press to indicate whether this color was the same or different from the color that had previously filled the probed circle (pressing “s” if it was the same color, or “d” if it was a different color). The presentation time, delay time, and response keys were the same for the color circle task and the spatial grid task—only the type of information being remembered (dot locations vs. circle color) varied between the location and color conditions. Observers were instructed to avoid verbal rehearsal strategies using the same instructions as Experiment 2A, except for the text “words” was replaced with “colors.” Additionally, observers were instructed to maintain central fixation throughout the experiment; although eye position was not monitored, we have no reason to

suspect that observers would adopt different fixation strategies for the various tasks (see Experiments 2A and 2B Discussion). Observers completed one block of spatial working memory trials (64 trials total, 32 within-hemifield trials and 32 between-hemifield trials randomly intermixed) and one block of color working memory trials (64 trials total, 32 within-hemifield trials and 32 between-hemifield trials randomly intermixed), the order of which was counterbalanced between observers. Immediately before each block of the main experimental trials, observers completed 16 practice trials that were identical to the main experimental trials, except that the empty grids (spatial working memory task) or empty circles (color working memory task) remained in place instead of moving to new locations.

Results

A 2 (hemifield movement: within vs. between) \times 2 (memory type: location vs. color) repeated-measures ANOVA revealed a significant hemifield movement \times memory type interaction ($F(1, 99) = 31.43$, $p < 0.001$, $d_z = 0.56$; see Figure 5A), as well as a significant main effect of hemifield movement ($F(1, 99) = 8.35$, $p = .005$) but no main effect of memory type ($F(1, 99) = 0.24$, $p = .62$). Again replicating Experiment 2A, for the spatial working memory task of remembering dot locations, observers were better at identifying target dots after vertical shifts within-hemifield ($M = 86.7\%$, $SD = 13.5\%$) than after horizontal shifts between-hemifield ($M = 81.4\%$, $SD = 13.2\%$; $t(99) = 6.26$, $p < 0.001$, $d_z = 0.63$). When the task required maintaining the color of circles in working memory, however, there was no significant difference in performance for vertical shifts within hemifield ($M = 83.8\%$, $SD = 10.5\%$) vs. horizontal shifts between hemifield ($M = 85.5\%$, $SD = 10.1\%$; $t(99) = 1.88$, $p = .06$, $d_z = -0.19$).

Experiment 3B: Modified color working memory task

In the color working memory task in Experiment 3A, after moving to a new quadrant, the probed circle was filled with either its original color or a new color that was not present in the original display. Therefore, observers could have potentially completed the task by remembering the originally presented circle colors and ignoring the circles' motion. Because this strategy would not have been effective for the spatial working memory task, the interaction observed in Experiment 3A could have been due to different strategies being used for the spatial and color working memory tasks, rather

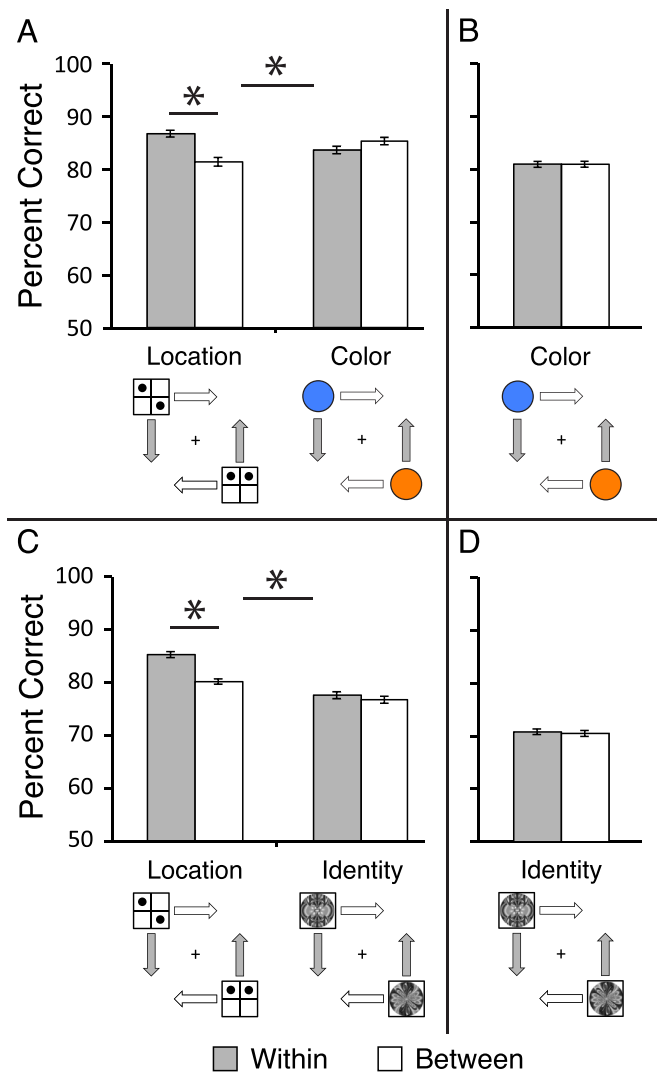


Figure 5. Results of Experiments 3A through 3D. Error bars represent within-subject SEM (Cousineau, 2005). (A) Observers displayed a between-hemifield cost for remembering dot locations (replicating Experiment 2A), but no performance difference was found for color working memory trials when items moved within vs. between the hemifields. (B) No between-hemifield cost was found for a modified version of the color working memory task, which required observers to bind each circle with its original color. (C) In addition to again replicating Experiment 2A (location conditions), no between-hemifield cost was found for remembering the identity of abstract fractals. (D) No between-hemifield cost was found for a modified version of the identity working memory task, which required observers to bind each square with its original image.

than due to differences in maintaining spatial vs. color information in working memory. To test this possibility, Experiment 3B used a modified version of the color working memory task in Experiment 3A, where the probed circle was filled with either its original color

(50% of trials), the original color of the unprobed circle (25% of trials), or a completely new color (25% of trials). Observers indicated whether or not the probed circle was filled with its original color, requiring observers to bind each circle with its respective color for successful completion of the task.

Methods

Participants

Sixty observers ($M_{\text{age}} = 37.5$, 37 male) were recruited via Amazon Mechanical Turk and participated after giving informed consent. This sample size was selected to match that of Experiment 2A, which was designed to have greater than 0.95 power to detect an effect of $d_z = 0.50$.

Stimuli

The stimuli were the same as those used for the color working memory task in Experiment 3A.

Procedure

The procedure was the same as for the color working memory task in Experiment 3A, except for one difference: instead of the probed circle being filled with either its original color (50% of trials) or a completely new color (50% of trials), in Experiment 3B the probed circle was filled either with its original color (50% of trials), the original color of the unprobed circle (25% of trials), or a completely new color (25% of trials).

Results

Consistent with the results of Experiment 3A, no significant difference was found when comparing within-hemifield trials ($M = 81.0\%$, $SD = 14.6\%$) and between-hemifield trials ($M = 80.8\%$, $SD = 13.7\%$; $t(59) = 0.15$, $p = .88$, $d_z = 0.02$). Additionally, in a post-hoc analysis aggregating the data from Experiment 3B with the data from the spatial working memory task in Experiment 2A, a mixed-factors ANOVA revealed a significant interaction of hemifield movement (within vs. between) and memory type (space vs. color; $F(1, 118) = 18.22$, $p < 0.001$).

There are two ways in which the results of Experiment 3B are consistent with observers binding each circle with its original color and tracking the circles as they move, rather than simply encoding the colors presented in the original display and ignoring the circles' motion. First, observers were far more likely to respond "same color" when the probed circle was filled with its original color ($M = 79.9\%$, $SD = 16.7\%$) than when it was filled with the unprobed circle's original color ($M = 15.7\%$, $SD = 20.7\%$, $t(59) = 16.04$, $p <$

0.001, $d_z = 2.07$); observers encoding the original colors but ignoring the circles' movement would have been equally likely to report "same color" for each of these trial types, because the probed color was in the original display in both cases. Second, observers were slightly (although not significantly) more likely to respond "same color" when the probed circle was filled with a completely new color ($M = 20.4\%$, $SD = 17.1\%$) than when it was filled with the unprobed circle's color ($M = 15.7\%$, $SD = 20.7\%$; $t(59) = 1.95$, $p = .06$, $d_z = 0.25$). Observers encoding the original colors and ignoring the circles' motion would have displayed the opposite pattern of data, because they would have been far more likely to mistakenly report the unprobed circle's color as the "same color" relative to a new color that had never been in the display. Together, these results are consistent with hemifield-specific maintenance in working memory for spatial information, but not color information.

Experiment 3C: Spatial vs. identity working memory

Experiments 3A and 3B demonstrated a crossover cost for maintaining spatial locations in working memory, but not color information. To test whether this dissociation may have resulted from the rehearsal of color names during working memory maintenance, Experiment 3C investigated whether a hemifield crossover cost would occur when maintaining the identity of abstract fractal images.

Methods

Participants

One hundred fifty observers ($M_{\text{age}} = 37.3$, 80 male) were recruited via Amazon Mechanical Turk and participated after giving informed consent. This sample size was selected using the results of pilot data ($N = 60$, interaction $d_z = 0.36$), and G*Power (Faul et al., 2009), which indicated that 150 observers would result in greater than 95% power to detect an interaction effect of $d_z = 0.30$.

Stimuli

The stimuli for the spatial working memory task were the same as those used in Experiments 2A, 2B, and 3A. For the fractal identity working memory task, stimuli were grayscale, circular fractal images (200×200 pixels); all other aspects of the display were the same as the spatial working memory task described in Experiment 2A (Figure 3). To match the number of unique spatial arrangements in the spatial working

memory task, six different fractal images (a subset of those used by Schapiro, Kustner, & Turk-Browne, 2012, converted to grayscale) were used for the fractal identity task.

Procedure

In addition to again completing the two experimental conditions described in Experiment 2A for the spatial working memory task, observers completed two new fractal identity conditions (Figure 3), requiring them to remember the identity of a fractal image presented in each hemifield. After the fractals were briefly presented inside a 200×200 pixel black square border (same timing parameters as the spatial working memory task described in Experiment 2A, only with fractal identity instead of dot locations), the fractals disappeared. The square black borders then shifted either vertically within their original hemifields or horizontally between hemifields. After the square borders reached their final locations, one square border was probed by being filled with a fractal image (either the fractal image that originally appeared within the probed border, or a new fractal image different from both of the originally presented fractals). Observers used a keyboard press to indicate whether this fractal was the same or different from the fractal that had previously occupied the probed square border (pressing "s" if it was the same fractal, or "d" if it was a different fractal). The presentation time, delay time, and response keys were the same for the spatial grid task and the abstract fractal task; only the type of information being remembered (dot locations vs. fractal identity) differed between the location and fractal identity conditions. Observers completed one block of spatial working memory trials (64 trials total, 32 within-hemifield trials and 32 between-hemifield trials randomly intermixed) and one block of fractal identity working memory trials (64 trials total, 32 within-hemifield trials and 32 between-hemifield trials randomly intermixed), the order of which was counterbalanced between observers. Immediately before each block of the main experimental trials, observers completed 16 practice trials that were identical to the main experimental trials, except that the empty grids (spatial working memory task) or empty square frames (fractal identity working memory task) remained in place instead of moving to new locations. Observers were instructed to avoid verbal rehearsal strategies using the same instructions as Experiment 2A.

Results

A 2 (hemifield movement: within vs. between) \times 2 (memory type: location vs. identity) repeated-measures ANOVA revealed a significant hemifield movement \times memory type interaction ($F(1, 149) = 14.55$, $p < 0.001$, $d_z = 0.31$; see Figure 5B), as well as significant

main effects of hemifield movement ($F(1, 149) = 23.27, p < 0.001$) and memory type ($F(1, 149) = 42.80, p < 0.001$). Again replicating [Experiment 2A](#), for the spatial working memory task of remembering dot locations, observers were better at remembering dot locations after within-hemifield shifts ($M = 85.1\%$, $SD = 16.6\%$) than after between-hemifield shifts ($M = 80.1\%$, $SD = 14.7\%$; $t(149) = 6.70, p < 0.001, d_z = 0.55$). When the task required maintaining the identity of abstract fractals in working memory, however, there was no significant difference in performance for within-hemifield shifts ($M = 77.4\%$, $SD = 14.4\%$) vs. between-hemifield shifts ($M = 76.5\%$, $SD = 13.1\%$; $t(149) = 0.95, p = .34, d_z = 0.08$).

Experiment 3D: Modified identity working memory task

Similar to the color working memory task in [Experiment 3A](#), after moving to a new quadrant, the probed square in [Experiment 3C](#) was filled with either its original fractal image or a new image that was not present in the original display. Therefore, observers could have potentially completed the task by remembering the originally presented images and ignoring the squares' motion within or between hemifields. Because this strategy would not have been effective for the spatial working memory task, the interaction observed in [Experiment 3C](#) could have been due to different strategies being used for the spatial and identity working memory tasks, rather than due to differences in maintaining spatial vs. identity information in working memory. To test this possibility, [Experiment 3D](#) used a modified version of the identity working memory task used in [Experiment 3C](#), where the probed square was filled with either its original image (50% of trials), the image originally presented in the unprobed square (25% of trials), or a completely new image (25% of trials). Observers indicated whether or not the probed square was filled with its original image, requiring observers to bind each square with its respective image for successful completion of the task.

Methods

Participants

Sixty observers ($M_{\text{age}} = 38.7$, 34 male) were recruited via Amazon Mechanical Turk and participated after giving informed consent. This sample size was selected to match that of [Experiment 2A](#), which was designed to have greater than 0.95 power to detect an effect of $d_z = 0.50$.

Stimuli

The stimuli were the same as those used for the identity working memory task in [Experiment 3C](#).

Procedure

The procedure was the same as for the identity working memory task in [Experiment 3C](#), except that instead of the probed square being filled with either its original image (50% of trials) or a completely new image (50% of trials), in [Experiment 3D](#) the probed square was filled either with its original image (50% of trials), the image originally presented in the unprobed square (25% of trials), or a completely new image (25% of trials).

Results

Consistent with the results of [Experiment 3C](#), no significant difference was found when comparing within-hemifield trials ($M = 70.8\%$, $SD = 16.6\%$) and between-hemifield trials ($M = 70.4\%$, $SD = 17.6\%$; $t(59) = 0.35, p = .73, d_z = 0.05$). Additionally, in a post hoc analysis aggregating the data from [Experiment 3D](#) with the data from the spatial working memory task in [Experiment 2A](#), a mixed-factors ANOVA revealed a significant interaction of hemifield movement (within vs. between) and memory type (space vs. identity; $F(1, 118) = 14.64, p < 0.001$).

Data from [Experiment 3D](#) were consistent with observers binding each square with its original image in two ways. First, observers were far more likely to respond “same image” when the probed square was filled with its original image ($M = 71.7\%$, $SD = 20.8\%$) than when it was filled with the unprobed square's original image ($M = 29.6\%$, $SD = 24.0\%$, $t(59) = 9.39, p < 0.001, d_z = 1.21$), despite the probed image being present in the original display for both of these trial types. Second, observers were slightly (although not significantly) more likely to respond “same image” when the probed square was filled with a completely new image ($M = 31.3\%$, $SD = 20.7\%$) than when it was filled with the unprobed square's image ($M = 29.6\%$, $SD = 24.0\%$, $t(59) = 0.82, p = .41, d_z = 0.11$). Observers encoding the original images and ignoring the squares' motion would have displayed the opposite pattern of data, because they would have been far more likely to mistakenly report the unprobed square's image as the “same image” than a new image that had never been in the display. Together, these results are consistent with hemifield-specific maintenance in working memory for spatial information, but not identity information.

Discussion: Experiments 3A through 3D

Observers displayed a between-hemifield crossover cost for a spatial working memory task, but not for color (Experiments 3A and 3B) or fractal identity (Experiments 3C and 3D) working memory tasks, suggesting that hemifield-specific control of working memory is specific to spatial information. These findings are related to previous research that found no bilateral field advantage for color working memory tasks without demands of spatial selection (Delvenne, 2005; Holt & Delvenne, 2014; Umemoto et al., 2010). Notably, these previous tasks did not require any updating of information, but instead only memory for the initial appearance of display items. However, our crossover task requires updating representations, binding initially presented items to new locations in the display. Previous research suggests that storage and updating have distinct underlying mechanisms (Pailian & Halberda, 2013). Combined with the present results, it seems that the lateralized component of working memory may be the mechanisms needed to update spatial representations. This conclusion is also consistent with previous findings of a larger bilateral field advantage for attentional tracking (Alvarez & Cavanagh, 2005) than for working memory (Delvenne, 2005), because attentional tracking likely has greater demands of spatial updating than working memory (Drew et al., 2011). Whether the mechanisms underlying the maintenance and updating of spatial working memory are partially distinct from, or entirely overlapping with, the mechanisms underlying attentional tracking remains an open question.

By asking observers to report whether probed stimuli were the same or different, the spatial and color working memory tasks used in the present study assessed recognition memory for spatial and identity information at a relatively coarse level. To investigate whether hemifield-specific control of working memory is specific to spatial information during a more fine-grained recall task, a continuous report paradigm could be used in a future study (e.g., Umemoto et al., 2010).

General discussion

Observers displayed between-hemifield crossover costs consistent with hemifield-specific control of spatial attention and working memory. Previous support for such hemifield-specific control in healthy individuals came primarily from findings of a bilateral field advantage (Alvarez & Cavanagh, 2005; Delvenne, 2005). Although a bilateral field advantage is consistent with hemifield-specific control of spatial attention

and working memory, it can also be explained by hemifield-limited spatial interference between target representations during early stages of visual processing (Franconeri et al., 2008; Franconeri et al., 2010; Liu et al., 2009; Störmer et al., 2014). Here we found a crossover cost for spatial attention and working memory, even when controlling for possible interference between items at the vertical midline between hemifields (unlike previous studies finding between hemifield costs; Gill & Alvarez, 2010; Minami et al., 2019), providing evidence for hemifield-specific control of each of these high-level processes critical to human cognition.

Importantly, the between-hemifield crossover costs for spatial tracking and working memory were not solely a consequence of spatial interference between low-level representations of target items, a factor we controlled in several ways. First, within- and between-hemifield trials were identical during the initial encoding of target information, ensuring that performance differences resulted from difficulty maintaining target information during between-hemifield movements, and not differences in spatial interference during encoding. Second, we ensured that the representations of target items did not interfere with each other when targets were near the hemifield border; we did this by including control experiments where targets moved to the vertical midline, but returned to their original locations instead of moving into the opposite hemifield (Experiments 1B and 2B). Because a performance decrease occurred only when targets crossed into the opposite hemifield, and not when they simply moved to the vertical midline, spatial interference between representations cannot be solely responsible for the between-hemifield crossover cost. Therefore, the between-hemifield crossover paradigm used in these experiments provides clear support for hemifield-specific processing beyond early sensory representation.

Unlike spatial working memory, a between-hemifield crossover cost was not found for maintaining color (Experiments 3A and 3B) or identity (Experiments 3C and 3D) information in working memory, suggesting that hemifield-specific control of working memory may be a unique signature of spatial processing. This result is consistent with dissociations between maintaining spatial vs. identity information in working memory (Courtney, Ungerleider, Keil, & Haxby, 1996; Mecklinger & Müller, 1996), as well as studies finding a bilateral field advantage only for tasks with spatial demands (Alvarez et al., 2012; Delvenne, 2005; Holt & Delvenne, 2014; Umemoto et al., 2010). Although we did not test for a between-hemifield crossover cost during the attentional tracking of identity features (Blaser, Pylyshyn, & Holcombe, 2000), previous demonstrations of feature-based attention extending between the hemifields (Saenz et al., 2003; Störmer & Alvarez, 2014) lead us to predict

that a between-hemifield crossover cost would not occur for identity feature-tracking tasks. This result would converge with our claim that hemifield-specific attentional control is a unique signature of spatial processing, whereas a crossover cost for an identity tracking task would suggest that hemifield-specific attentional control occurs whenever tasks have high demands of attentional updating.

Importantly, although we provide evidence for hemifield-specific control of attention and working memory (and thus evidence against these processes being limited exclusively by spatial interference), our results do not conflict with models of spatial interference at early stages of visual processing (Ahmad et al., 2017; Franconeri et al., 2013; Scalf & Beck, 2010; Scalf et al., 2013; Störmer et al., 2014; Torralbo & Beck, 2008). These previous findings have clearly demonstrated that attention and working memory are limited by spatial interference within each hemifield; thus, we speculate that each hemifield-specific control system is limited by spatial interference within its own hemifield. Similarly, although our results raise the possibility that hemifield-specific control of attention and working memory may contribute to previous findings of a bilateral field advantage, they do not directly inform whether this phenomenon is due to exclusively spatial interference or a combination of spatial interference and hemifield-specific control. For example, hemifield-specific control may only occur for relatively complex tasks (Banich & Belger, 1990; Weissman & Banich, 2000), such as when objects are moving, but not for relatively simple tasks, such as when objects remain stationary.

Mechanisms of the crossover cost

The present findings allow several inferences regarding the mechanisms of control over each hemifield. For example, control of spatial processing within each hemifield cannot be completely independent of the other hemifield, because observers performed well above chance (50%) during between-hemifield movements, indicating that at least partial information about target locations can be shared between the hemifields. There are at least two possibilities for why information sharing between hemifield-specific control systems would be imperfect, producing between-hemifield crossover costs. One possibility is that each hemifield has a separate high-level representational buffer for maintaining target locations (Franconeri, Alvarez, & Cavanagh, 2013). Exchanging information between these buffers could require each buffer to temporarily represent information from both hemifields during between-hemifield movements, a “soft handoff” of information, consistent with electrophysiological findings (Drew

et al., 2014). Simultaneous representation of both the target departing a buffer’s hemifield and the target arriving from the opposite hemifield could allow hemifield-specific buffers to exchange their information; this information exchange would be imperfect, however, due to interference arising from both targets being temporarily represented within each buffer as represented information crossed between the hemifields. By this account, representational overlap (Fendrich et al., 1996) and spatial interference at the border between hemifields could be the result of hemifield-specific control, providing hemifield-specific control systems with a way to avoid complete information loss as information moves between the hemifields. Separate representational buffers for each hemifield could also produce a crossover cost if coordination between buffers is more taxing than maintaining information within separate buffers, which may result in failure to transfer targets between buffers on a subset of between-hemifield trials.

A second possibility for how information might be shared between hemifield-specific control systems is primarily within-hemispheric deployment of attentional pointers from bilateral control areas (e.g., parietal cortex; Battelli, Alvarez, Carlson, & Pascual-Leone, 2009; Culham et al., 1998; Howe, Horowitz, Akos Morocz, Wolfe, & Livingstone, 2009) to earlier representational areas. Such biased deployment would result in attentional pointers primarily controlling the selection of contralateral targets, but still having some control over ipsilateral targets. When items cross between hemifields, the contralateral bias would require the attentional pointers to begin primarily tracking the previously ipsilateral targets, which they had only limited control over. By this account, the between-hemifield crossover cost would arise from a shifting of priority over which targets were being tracked, and not from a temporary representation of both hemifields producing interference. This possibility is consistent with evidence finding primarily contralateral control over attentional tracking when items are presented in both hemifields, but the ability of ipsilateral attentional mechanisms to contribute to tracking when the contralateral system is disrupted with transcranial magnetic stimulation (Battelli et al., 2009). Because both the separate representational buffers and contralateral bias accounts of hemifield-specific control are consistent with between-hemifield crossover costs, future work is needed to clarify the precise mechanisms of information transfer between hemifields.

Relationship to patient findings

The behavior of hemispatial neglect patients (Posner, Walker, Friedrich, & Rafal, 1984) and split-brain patients (Luck et al., 1989, 1994) has previously

established the capability of the cerebral hemispheres to separately control high-level processing in each hemifield. The present study offers the clearest demonstration to date that hemifield-specific attentional control is present in healthy individuals as well, because healthy observers displayed a between-hemifield crossover cost incompatible with a single attentional focus. Although our behavioral findings do not directly inform the neural underpinnings of hemifield-specific attentional processing, we speculate that crossover costs in healthy individuals and the behaviors of these patient populations share a common origin: specialized processing of the contralateral hemifield by each cerebral hemisphere. However, the precise relationship between the cognitive architecture producing crossover costs and the neural architecture underlying the behavior of these patient populations remains unclear, because the consequences of hemifield-specific control likely vary greatly with changes to neural structure. For example, hemispatial neglect seems to result from an interhemispheric imbalance arising from damage to one hemisphere (Corbetta & Shulman, 2011), whereas crossover costs occur despite both hemispheres functioning normally.

Additionally, the study of hemispatial neglect patients suggests that the left cerebral hemisphere has a strong contralateral bias and primarily represents the right hemifield, whereas the right cerebral hemisphere may have a more global representation of both hemifields (Mesulam, 1999), a possibility that is also supported by research in healthy individuals (Sheremata, Bettencourt, & Somers, 2010). For the present study, a more global representation by the right hemisphere leads to two predictions: 1) for within-hemifield trials, there should be a right hemifield advantage, as this hemifield would be represented by both cerebral hemispheres, and 2) for between-hemifield trials, there should be an advantage for targets that move from the left hemifield to the right hemifield (vs. the opposite direction), as the right hemisphere could continue to represent its targets even after they move to the right hemifield. Our results are only partially consistent with these predictions. Observers in Experiments 1A and 1B had a right hemifield advantage during within-hemifield trials, ($M_{\text{left}} = 75.7\%$, $M_{\text{right}} = 81.0\%$, $t(55) = 3.06$, $p = .003$, $d_z = 0.41$), consistent with previous findings of a right hemifield advantage for multiple object tracking (Holcombe et al., 2014). However, this difference was not found for the spatial working memory task used in Experiments 2 and 3, where instead there was a small left-hemifield advantage, ($M_{\text{left}} = 86.5\%$, $M_{\text{right}} = 84.8\%$, $t(309) = 2.50$, $p = .01$, $d_z = 0.14$). Additionally, no differences were found for between-hemifield trials when targets moved between hemifields from left to right vs. right to left, for either the spatial tracking task, (left to right $M = 68.1\%$, right to left $M = 68.8\%$, $t(55) = 0.41$, $p = .69$,

$d_z = 0.05$), or the spatial working memory task, (left to right $M = 79.8\%$, right to left $M = 80.7\%$, $t(309) = 1.20$, $p = .23$, $d_z = 0.07$). Because our results do not conclusively map onto predictions motivated by hemispatial neglect research, future work exploring the neural mechanisms of hemifield-specific control will be necessary to draw more clear connections between hemifield-specific processing in healthy individuals and the deficits of patient populations.

Why have hemifield-specific control?

Although the present study provides evidence for hemifield-specific control of spatial attention and working memory, it does not directly address why such independent processing might occur. Computational modeling has indicated that hemisphere-specific processing may minimize the impact of brain damage, because having both hemispheres capable of performing the same computation could allow relatively normal functioning as long as one hemisphere remained intact (Schapiro, McClelland, Welbourne, Rogers, & Lambon Ralph, 2013); hemifield-specific control of attention and working memory may result from such bilateral processing. Additionally, computational modeling has suggested that hemispheric specialization (e.g., greater control of verbal processing in the left hemisphere) could allow more efficient information processing (Jacobs, 1999), a possibility supported by correlations between hemispheric specialization and measures of cognitive function (Gotts et al., 2013). Although speculative, hemifield-specific control may be necessary for hemispheric specialization to occur, a possibility that could be explored in future work exploring associations between hemifield-specific control, hemispheric specialization, and cognitive performance.

Although plausible, these explanations do not easily explain why hemifield-specific processing would be specific to spatial information (but not identity information such as color or texture information). We speculate that this dissociation may be related to differences in the functional relevance of spatial vs. identity information, which are processed separately (to some degree) in the dorsal and ventral streams of the visual system, respectively (Goodale & Milner, 1992; Goodale, Milner, Jakobson, & Carey, 1991; Ungerleider & Mishkin, 1982). Whereas behavioral responses to identity information are likely to be consistent regardless of an object's location in the visual field (e.g., one would likely make the decision to run away from a lion regardless if the lion were in the left or right visual field), responses to spatial information often involve making a motor response to a specific spatial location with one side of the body (which, like the brain, is bilateral). For example, responding to an

incoming punch to the right side of the head requires efficient detection of the punch's location and an appropriate motor response—accidentally responding by blocking the left side of the head would have negative consequences. Nonspatial visual information (such as the color of a boxing glove) rarely requires a response to a specific location or with a particular side of the body, perhaps resulting in less hemifield-specific processing of identity information. Consistent with this possibility, processing spatial information seems to rely primarily on neural connectivity within the individual cerebral hemispheres, whereas processing identity information relies more equally on connections both within and between hemispheres (Cohen & Maunsell, 2011; Mishkin & Ungerleider, 1982). Although speculative, the possibility of lateralization for action could be explored in future studies testing whether location-specific action generation becomes more efficient as spatial attention becomes more lateralized.

An index of hemifield-specific processing

The between-hemifield crossover paradigm used in this study has the potential to be used for better understanding what other tasks use hemifield-specific control. For example, a bilateral field advantage has been found for voluntary control of visual awareness, because it is easier to perceive two pairs of ambiguously moving dots as moving in different directions (e.g., one dot pair moving vertically and one pair moving horizontally) when the dot pairs are in separate hemifields than when the pairs are in the same hemifield (Nothelfer, Suzuki, & Franconeri, 2015). However, it is unclear whether this result reflects separate high-level control of visual awareness for each hemifield or instead results from hemifield-limited spatial interference during encoding. These two possibilities could be differentiated with a hemifield-crossover design where observers must maintain distinct perceptions of ambiguous stimuli that move either within or between the hemifields; more difficulty maintaining distinct perceptions during between-hemifield movements would provide evidence for hemifield-specific control of visual awareness.

The between-hemifield crossover paradigm is also an easily administered behavioral task, potentially allowing its use for measuring whether hemifield-specific processing changes throughout the lifespan (Blankenship, Strong, & Kibbe, 2020). Hemispheric specialization has been hypothesized to develop throughout childhood (Behrmann & Plaut, 2015) before decreasing at older ages (Cabeza, 2002). A similar developmental trajectory for hemifield-specific processing would provide evidence that these phenomena are related. Given evidence

of an association between hemisphere-specific processing and cognitive functioning (Gotts et al., 2013), better understanding the development and importance of hemifield-specific processing could influence interventions hoping to maximize cognitive performance.

Conclusions

The between-hemifield crossover costs found in the present study provide evidence for hemifield-specific control of spatial attention and working memory, overcoming the limitations of previous behavioral studies that could not differentiate between hemifield-specific control and hemifield-limited spatial interference. Together with the lack of a crossover cost when remembering identity features, these results suggest that hemifield-specific control is a unique signature of spatial processing. We hope that these results will motivate future work exploring the origins and benefits of hemifield-specific processing, as well as further investigations into the mechanisms of information transfer between the hemifields.

Keywords: hemifield, attention, working memory, crossover costs, bilateral field advantage

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