Anatomical constraints on attention: Hemifield independence is a signature of multifocal spatial selection

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Previous studies have shown independent attentional selection of targets in the left and right visual hemifields during attentional tracking (Alvarez & Cavanagh, 2005) but not during a visual search (Luck, Hillyard, Mangun, & Gazzaniga, 1989). Here we tested whether multifocal spatial attention is the critical process that operates independently in the two hemifields. It is explicitly required in tracking (attend to a subset of object locations, suppress the others) but not in the standard visual search task (where all items are potential targets). We used a modified visual search task in which observers searched for a target within a subset of display items, where the subset was selected based on location (Experiments 1 and 3A) or based on a salient feature difference (Experiments 2 and 3B). The results show hemifield independence in this subset visual search task with location-based selection but not with feature-based selection; this effect cannot be explained by general difficulty (Experiment 4). Combined, these findings suggest that hemifield independence is a signature of multifocal spatial attention and highlight the need for cognitive and neural theories of attention to account for anatomical constraints on selection mechanisms.

Keywords: attention, multifocal, hemifield effect, visual search

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Introduction

The world consists of an abundant and continuously changing flow of visual information. With attention, we take an active role in how we experience this stream of input as meaningfully segmented objects and events. Increasing attention to a target item gives it greater clarity (Titchener, 1908), higher contrast (Carrasco, Ling, & Read, 2004; Prinzmetal, Nwachuku, Bodanski, Blumenfeld, & Shimizu, 1997), and enhanced highspatial frequency response (Carrasco, Williams, & Yeshurun, 2002; Yeshurun & Carrasco, 1998). We are also able to perceive attended objects as persisting entities (i.e., as the same object over changes in time, space, and physical appearance) as long as those objects exhibit spatiotemporal continuity (Kahneman, Treisman, & Gibbs, 1992; Mitroff & Alvarez, 2007; Scholl, 2007). Thus, attention is used to manage the flow of information from low-level perceptual processes to higher level cognition, enabling us to experience a

rich and continuous representation of a small subset of objects and events.

Although attentional selection is generally considered a high-level cognitive function, there appear to be important low-level, anatomical constraints on attentional processing. Indirect evidence for these anatomical constraints comes from a large literature showing various visual field effects on attentional selection. For example, there are a variety of asymmetries in attentional processing across the visual field, such as the coarser spatial resolution of attention in the upper visual field than in the lower visual field (He, Cavanagh, & Intriligator, 1996; Intriligator & Cavanagh, 2001) and the enhanced ability to maintain sustained focal attention along the horizontal meridian relative to the vertical meridian (Mackeben, 1999). The upper-lower asymmetry is likely to be associated with visual areas in which the lower visual field is overrepresented. In monkeys, there is an upper-lower asymmetry that increases from relatively modest in primary visual cortex (V1; Tootell, Switkes, Silverman,

& Hamilton, 1988) to much more pronounced in higher visual areas such as middle temporal cortex (MT; Maunsell & Van Essen, 1987) and parietal cortex (Galletti, Fattori, Kutz, & Gamberini, 1999). The horizontal–vertical meridian asymmetry is likely to be linked to the relatively lower density of ganglion cells along the vertical meridian relative to the horizontal meridian (Curcio & Allen, 1990; Perry & Cowey, 1985) and possibly to the accelerated decline of cone density with eccentricity along the vertical meridian relative to the horizontal meridian (Curcio, Sloan, Packer, Hendrickson, & Kalina, 1987).

There is some disagreement as to whether these asymmetries should be considered effects of attentional processing or lower level visual constraints (Carrasco, Talgar, & Cameron, 2001). However, other attentional effects, such as interference effects between targets and distractors, or targets and other targets, also show an influence of boundaries within the visual field (Alvarez & Cavanagh, 2005; Carlson, Alvarez, & Cavanagh, 2007). For example, attended targets interfere with each other more when they both appear within the same quadrant of the visual field than when they appear the same distance apart but in separate quadrants of the visual field (Carlson et al., 2007). It is likely that this quadrant-level effect is linked to visual areas that maintain separate representations of the quadrants of the visual field, such as visual areas V2 and V3 (DeYoe et al., 1996; Engel, Glover, & Wandell, 1997; Sereno et al., 1995; Tootell et al., 1995; Zeki, 2003).

One particularly dramatic demonstration of a visual field effect on attentional processing is the hemifield independence observed in attentional tracking (Alvarez & Cavanagh, 2005). In this attentional tracking task, observers kept their eyes focused at the center of the display and attentively tracked moving targets in one of the four quadrants of the peripheral visual field. Surprisingly, observers could keep track of twice as many targets when they appeared in separate halves of the visual field (e.g., in the top left and top right quadrants) than when they appeared in the same half of the visual field (e.g., in the top right and bottom right quadrants). It was as if the attentional processes required to track a moving object could operate independently in the left and right visual hemifields. This degree of independence is surprising since attentional selection is often considered to be limited by a unified higher level control system (Broadbent, 1958; Ellenberg & Sperry, 1979; Kahneman, 1973; Luck, Hillyard, Mangun, & Gazzaniga, 1989), and hemifield representations are characteristic of lowerlevel visual areas (see Bullier, 2004). Moreover, other tasks that putatively require visual spatial attention do not show hemifield independence. Specifically, visual search tasks do not show any hemifield effects in normal, healthy observers (Luck et al., 1989). For example, when searching for a target object among

distracting objects, reaction time is unaffected by the location of the items in the visual field. Participants can find the target just as quickly when the items are divided between the visual fields (e.g., in the top left and top right quadrants) as when they all appear in the same half of the visual field (e.g., in the top right and bottom right quadrants).

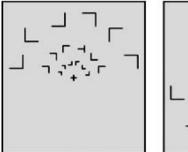
Cognitive scientists can use visual field effects combined with knowledge of the underlying neural architecture to constrain cognitive theories (for a recent example, see Torralbo & Beck, 2008). The current study explores the boundary conditions in which hemifield independence is observed in visual selective attention tasks, in order to dissect attention and understand when dividing attention across hemifields is more efficient than dividing attention within a hemifield. One obvious stimulus difference between attentive tracking and visual search tasks is that the objects in the tracking task move whereas the objects in a visual search task are stationary. Beyond this stimulus difference, a potentially important processing difference between attentive tracking and visual search is the demand for sustained multifocal attention (Cavanagh & Alvarez, 2005). In attentive tracking, participants must continuously attend to multiple target items and ignore a subset of distracting items. In contrast, in the typical visual search task, all items are potential targets until they are identified as nontargets, and the task does not require actively attending to multiple items while ignoring multiple other items simultaneously.

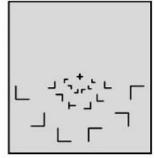
The current study focuses on the role that sustained, multifocal attention plays in hemifield independence. To preview the results, we found that a visual search task that requires sustained multifocal attention shows hemifield independence, but only when items are selected based purely on their locations (Experiments 1 and 3A) and not when they are selected based on their features (Experiment 2 and 3B). We also found that general task difficulty does not drive hemifield independence in visual search (Experiment 4). These findings suggest that hemifield independence is a signature of multifocal spatial attention, which has important implications for understanding the role of anatomy in attentional processing and for the operation of attention at the interface between low-level processing and high-level visual cognition.

Experiment 1: A visual search task requiring location-based selection shows hemifield independence

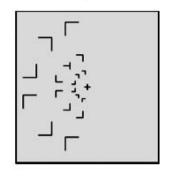
A subset visual search task was employed to test whether hemifield independence occurs when location-

Bilateral Displays





Unilateral Displays



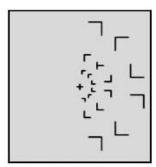


Figure 1. Example bilateral and unilateral search displays. Participants fixed the "+" at the center of the display and searched for the target letter T. The task was to indicate the orientation of the T as quickly and as accurately as possible. On bilateral trials, items appeared in either the upper or the lower visual field. On unilateral trials, items appeared in either the left or right visual field. The absolute location of the target in the visual field was balanced across these conditions (e.g., a target was equally likely to appear at the location just above and to the right of fixation in both the bilateral and unilateral displays).

based attentional selection is required. Figure 1 illustrates the hemifield manipulation (bilateral versus unilateral displays), and Figure 2 shows sample trials for the spatial subset search and standard search. At the beginning of a spatial subset search trial, several black placeholders were presented and a subset of them where cued by turning white for 0.5 second. Following the cues, all items appeared black for 1 second, which was sufficiently long to be out of the range of any exogenous attentional capture caused by the luminance change (Nakayama & Mackeben, 1989). During this interval, participants were required to focus their attention on the cued locations so they could limit their search to those positions. Then segments of the placeholders disappeared, revealing letters. All of the letters were distractor Ls, except for one target T that was tilted either clockwise or counterclockwise by 90°. The target always appeared within the cued subset, and the task was to indicate the target orientation as quickly as possible without sacrificing accuracy.

The critical manipulation was the location of the items in the visual field. Items were always equally divided between two quadrants, as were the cued locations. For example, if the cued set size were 4, there would be 2 cued locations in each quadrant. In the bilateral condition, items appeared in either the upper or the lower visual field. In the unilateral condition, items appeared in either the left or the right visual field (see Figure 1). It is important to note that each quadrant was tested equally often in the bilateral and the unilateral conditions, so across trials the two conditions were perfectly matched in terms of the absolute spatial location occupied by the letters. The only difference between these two conditions was whether the two filled

quadrants within a trial were in separate hemifields (bilateral) or within the same hemifield (unilateral).

If location-based selection underlies hemifield independence, we should see faster processing of bilateral displays than of unilateral displays in this subset search task. For comparison, we also included a standard visual search in which only 2, 4, 6, 8, or 10 items appeared, and all were potential targets. This standard search task does not require filtering a subset of positions based on location as the subset search task does. Thus, if sustained selection plays a key role in hemifield independence, the standard search task should show no difference between bilateral and unilateral displays, as has been observed previously (Luck et al., 1989).

Method

Participants

Participants were author GA and 13 naïve observers who gave informed consent, had normal or corrected-to normal vision, and were paid or received course credit.

Stimuli

The stimuli are shown in Figure 2. For the subset search task, a black fixation cross $(1.2^{\circ} \times 1.2^{\circ})$ was always present. At the beginning of each trial, 18 waffle-shaped placeholders were presented, with 6 placeholders each at 3 different eccentricities. The size of items scaled with distance from fixation (sizes were $0.6^{\circ} \times 0.6^{\circ}$, $1.2^{\circ} \times 1.2^{\circ}$, $2.4^{\circ} \times 2.4^{\circ}$, at distances from fixation of 2.5° , 5° , and 10° , respectively) to equate the visibility of the items

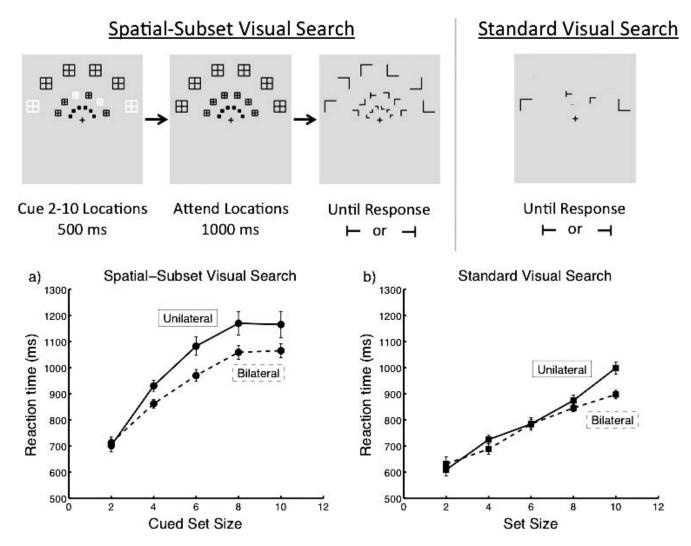


Figure 2. Displays and results of Experiment 1. The top panel illustrates sample trials of the spatial subset search task and the standard search task. The bottom panel shows reaction time (ms) versus set size for correct responses on each task. Error bars show within-subject standard error of the mean. (a) In the spatial subset visual search task, reaction times are longer in the unilateral condition than in the bilateral condition, with a reliable difference emerging at set size 4. (b) In the standard visual search task, there was no difference between unilateral and bilateral displays, except at the largest set size.

at each location in the display. The placeholders could appear in a bilateral alignment (either in the upper or lower visual field) or in a unilateral alignment (in the left or right visual field). At the beginning of each trial, 2, 4, 6, 8, or 10 target locations were cued by turning white for 500 ms, then all placeholders appeared black for 1000 ms. Finally, segments of the placeholders disappeared to reveal letters. One search target, the letter T rotated either clockwise or counterclockwise by 90°, appeared within the cued subset and the remaining 17 letters were distractor Ls randomly oriented 0°, 90°, 180°, or 270° from vertical. The test display remained present until the observer responded (as was the case in all experiments and conditions reported in the present paper).

Participants also performed a standard visual search in which there were no placeholders, and 2, 4, 6, 8, or 10 items appeared. These search displays looked identical to the search displays for the subset search task, except the irrelevant letters were not present.

Procedure

Participants pressed a key to initiate each trial. Then the 500-ms cue display appeared, followed by a 1000-ms placeholder display. Participants were instructed to focus their attention on the cued positions and were informed that the target would appear within the cued subset. The cues were 100% valid. Because the delay between the cue and test was so long (1000 ms), there was no transient signal or other physical difference between the cued locations and the uncued locations. Thus, participants were required to maintain a top-down attentional filter, focusing their attention on the cued locations and ignoring the uncued locations.

Set size	Spatial subset		Standard	
	Bilateral	Unilateral	Bilateral	Unilateral
2	3.6 (1.1)	1.8 (0.6)	2.7 (0.8)	1.8 (0.7)
4	3.6 (1.2)	2.1 (0.6)	2.1 (0.7)	1.2 (0.5)
6	3.6 (1.2)	2.4 (0.9)	3.0 (0.8)	1.5 (0.6)
8	3.0 (1.2)	2.1 (1.0)	1.5 (0.7)	3.3 (1.1)
10	1.2 (0.5)	0.9 (0.7)	1.2 (0.5)	1.2 (0.7)
Average	3.0 (0.6)	1.9 (0.5)	2.1 (0.3)	1.8 (0.3)

Table 1. Error rate for each condition in Experiment 1.

Finally, segments of the placeholders disappeared to reveal letters. The task was to find the T and report its orientation as quickly and as accurately as possible. Participants completed 480 trials with 2 search tasks (subset search versus standard search), 5 set sizes (2, 4, 6, 8, or 10), and hemifield alignment (bilateral versus unilateral) randomly mixed within the session.

Results

Overall error rates were low (less than 3%; see Appendix, and Table 1) and did not differ between bilateral and unilateral displays (t[13] = 1.51, p = 0.255, $r^2 = .15$). Given the low error rates, the following analysis focuses on reaction time for trials in which participants responded correctly.

As shown in Figure 2, there was a reliable hemifield effect (bilateral reaction time was faster than unilateral reaction time), but the effect was small in the standard search task (Figure 2b) and was most pronounced at the largest set size. In contrast, the effect of hemifield alignment was greater and emerged at smaller set sizes in the subset search task (Figure 2a).

An analysis of variance (ANOVA) was run on reaction time with search task (subset versus standard), set size (2, 4, 6, 8, 10), and alignment (bilateral versus unilateral) as factors. Overall, reaction time was slower in the subset search task $(F[1,13] = 60.7, p < 0.001, \eta^2 =$.82), indicating that there was a cost to filtering out irrelevant items in the subset search task. Most importantly, there was a main effect of hemifield alignment $(F[1,13] = 25.1, p < 0.001, \eta^2 = .66),$ indicating that reaction time was significantly slower in the unilateral condition than in the bilateral condition. This effect was stronger in the subset search task (greater separation between lines in Figure 2a than in Figure 2b), which is supported by the significant interaction between task and hemifield alignment $(F[1,13] = 5.4, p = 0.037, \eta^2 = .29).$

A separate ANOVA on the standard search task data showed that there was a significant effect of hemifield alignment (F[1,13] = 17.13, p = 0.001, $\eta^2 = .57$). This effect was not significant with set size 10 excluded from the analysis (F[1,13] = 2.03, p = 0.178, η^2

= .14), suggesting that the overall effect was driven primarily by the trend at set size 10.

Discussion

In the standard visual search task, all items are potential targets and there is no reason to split attention and inhibit a particular subset of the items. Consistent with previous research (Luck et al., 1989), we find that in the standard search task, without spatial selection demands, there is very little effect of dividing items between the left and right hemifields, except at the largest set size. The emergence of an effect for the largest set size in the standard search task may reflect increased crowding with increased set size. Crowding between elements within a hemifield is greater than across hemifields, even with the same physical separation between items (Chakravarthi & Cavanagh, 2006). In contrast, the subset visual search task explicitly requires observers to split their attention, to select the cued placeholders, and to filter out the irrelevant items in the display. Under these conditions of sustained multifocal attention, there was a large, reliable advantage for dividing items between the left and right hemifields. Observers can search through a subset at a faster speed when the items are divided between the left and right hemifields (at the top or bottom of the display) than when they all appear within a single hemifield (in the left or right visual field). Critically, the absolute spatial location of items was perfectly matched across trials for the bilateral and unilateral displays, and thus these effects cannot be explained by differences in location or local crowding effects.

In the current study, the subset had to be selected using location-based attention because the cued items were physically identical to the uncued items during the 1000 ms preceding the appearance of the search stimuli. Thus, there was no featural difference between the cued locations and the uncued locations that could be used to selectively attend to the cued positions. In Experiment 2, we tested whether a hemifield effect would be observed when the selection could be made based on a salient feature difference.

Experiment 2: A visual search task requiring feature-based selection does not show hemifield independence

A subset visual search task was employed to test whether hemifield independence occurs when featurebased attentional selection is required. Unlike in

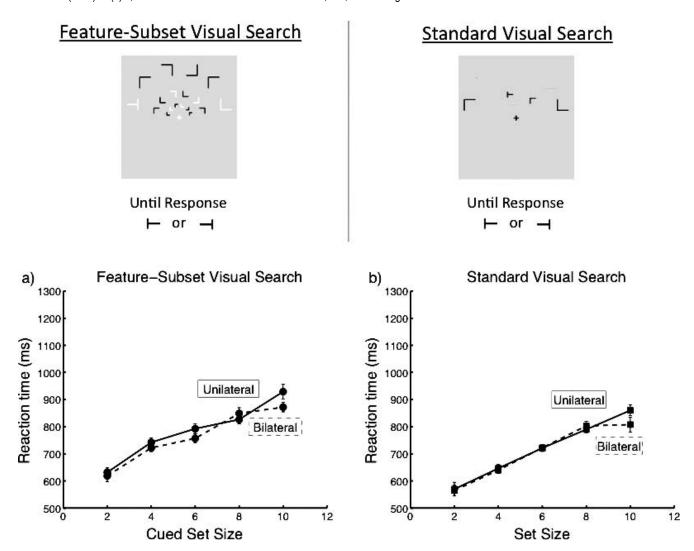


Figure 3. Displays and results of Experiment 2. The top panel illustrates sample trials of the feature subset search task and the standard search task. The bottom panel shows reaction time (ms) versus set size for correct responses on each task. Error bars show within-subject standard error of the mean. (a) In the feature subset visual search task there was no consistent difference between unilateral and bilateral displays. (b) In the standard visual search task, there also was no consistent difference between unilateral and bilateral displays.

Experiment 1, the subset in this experiment was defined by a salient feature difference (see Figure 3). Specifically, all of the relevant search items appeared white and the irrelevant items appeared black throughout the subset search trials. The target always appeared within the white subset, and the task was to indicate the target orientation as quickly as possible without sacrificing accuracy.

As in Experiment 1, the critical manipulation was the location of the items in the visual field. In the bilateral condition, items appeared in either the upper or the lower visual field. In the unilateral condition, items appeared in either the left or the right visual field. If feature-based selection underlies hemifield independence, we should see faster processing of bilateral displays than unilateral displays in this subset search task. However, if hemifield independence is a signature of location-based attentional selection, then the hemifield effect should be no different

for a feature-based subset search than for a standard visual search task. Thus, for comparison, we again included a standard visual search in which only 2, 4, 6, 8, or 10 items appeared.

Method

Participants

Participants were author GA and 9 naïve observers who gave informed consent, had normal or corrected-to normal vision, and were paid or received course credit.

Stimuli

Displays were identical to Experiment 1 except that the fixation point was white and the relevant subset of items was white throughout subset search trials.

	Feature subset		Standard	
Set size	Bilateral	Unilateral	Bilateral	Unilateral
2	3.3 (1.2)	2.1 (1.3)	5.0 (2.1)	3.3 (2.1)
4	2.9 (1.8)	4.6 (1.9)	3.0 (1.4)	2.1 (0.7)
6	5.1 (1.9)	2.1 (0.9)	5.4 (1.5)	1.7 (0.7)
8	3.8 (2.0)	2.6 (0.9)	4.6 (1.2)	1.7 (0.9)
10	5.2 (2.4)	5.5 (2.3)	5.5 (2.2)	1.7 (1.3)
Average	4.1 (1.5)	3.4 (1.1)	4.7 (1.3)	2.1 (0.5)

Table 2. Error rate for each condition in Experiment 2.

Procedure

The procedure was identical to that of Experiment 1 except that there was no precue display. Each subset search trial began with a 500-ms fixation display, followed by the onset of the search array. There were 2 to 10 white items and the remaining items (total of 18) were black. Standard search trials were identical except that the irrelevant black items were not presented.

Results

Although overall errors were higher in the bilateral condition (M=4.4%, SEM=1.3) than in the unilateral condition (M=2.7%, SEM=0.7; F[1,9]=6.5, p=0.03, $\eta^2=.42$), the error rates were low and did not depend on task (F[1,9]=3.1, p=0.1, $\eta^2=.26$) (see Appendix, and Table 2). Thus, there does not appear to be evidence that speed–accuracy tradeoffs could contribute to differences between tasks, and the following analysis focuses on reaction time for trials in which participants responded correctly.

As shown in Figure 3, there was no reliable hemifield effect in either the subset search task (Figure 3a) or the standard search task (Figure 3b), although there was a trend for a bilateral advantage at the largest set size for both tasks.

An ANOVA was run on reaction time with search task (subset versus standard), set size (2, 4, 6, 8, 10), and hemifield alignment (bilateral versus unilateral) as factors. Overall, reaction time was slower in the subset search task $(F[1,9] = 48.5, p < 0.001, \eta^2 = .84)$, indicating that there was a cost to filtering out irrelevant items in the subset search task. Most importantly, the main effect of hemifield alignment was only marginal $(F[1,9] = 5.02, p = 0.052, \eta^2 = .36)$ and there was no hint of an interaction between search task and hemifield alignment (F < 1).

Discussion

Unlike the location-based subset search used in Experiment 1, the feature-based subset search task

showed little evidence of a hemifield effect in visual search. At the largest set size, there was a trend for a hemifield effect (faster reaction time for bilateral than for unilateral displays), but this effect was comparable for the subset search and the standard search task. The feature-based search task certainly requires dividing attention between multiple items, attending to the selected subset, and ignoring the irrelevant subset. Thus, hemifield independence does not appear to be a characteristic of just any type of multifocal attentional selection. Instead, it seems that hemifield independence is most likely to arise under conditions in which location-based attentional selection is required.

Experiment 3A: Controlling for the role of precueing and spatial working memory in the spatial subset search task

Combined, Experiments 1 and 2 suggest that hemifield independence is observed when multifocal spatial selection is required to perform a visual search task. However, the spatial subset visual search task was also the only task that had precues to specify the target locations. It is possible that these precues provided time to set up multifocal attention (i.e., split foci of attention), which is known to be more efficient across hemifields (Alvarez & Cavanagh, 2005; Awh & Pashler, 2000). On this account, hemifield independence is not a signature of spatial attention but of multifocal attention, and therefore providing precues in the feature subset search and standard visual search tasks should also give rise to a hemifield effect.

Another cue-related concern is that the precues create a spatial working memory load in the subset search condition, making it unclear whether it was the spatial memory load or the spatial selection demands that caused the hemifield effect. As shown in Figure 2, observers were required to search among a subset of locations where the subset was cued at the start of each trial and then the locations of the subset were remembered for the duration of the trial. It is possible that this memory load, and not the selection demands of the subset search task, caused the hemifield effect observed in Experiment 1. This concern is reinforced by previous research, which suggests that there is some degree of independence between the hemifields in spatial working memory but not in featural working memory (Delvenne, 2005).

However, there are some reasons to doubt the possibility that spatial working memory load caused the observed hemifield effect. First, accuracy rates in Experiment 1 were very high, suggesting that remem-

bering the locations of the cued subset was not a major source of difficulty on the task (presumably because the placeholders were continuously visible and not being remembered in the absence of visual input). Second, in Delvenne (2005) the spatial working memory task combined selection demands with memory demands because the to-be-remembered items were presented simultaneously. Thus, it is possible that limitations in the initial encoding of items, not in the storage of those items, caused the hemifield effect observed in this previous study.

Despite these counterarguments, Experiment 3A sought to eliminate the possible working memory confound by replicating Experiment 1 without the need to remember the locations of the target subset. Rather than cueing a random subset of possible locations, participants knew on each trial that the target could ever appear only in the middle ring of letters (see Figure 4). This middle ring was surrounded by task-irrelevant flankers positioned along an inner and outer ring, and masks were placed on the vertical and horizontal midlines at all eccentricities to increase the spatial selection demands. In the standard search task, only this middle ring of task-relevant letters was presented, and no task-irrelevant flankers or masks were ever presented.

If the hemifield effect observed in the subset search condition of Experiment 1 was due to a spatial working memory load, then no hemifield effect should be observed in the present experiment because there is no spatial working memory load. If the hemifield effect was due to having time to set up multifocal attention, then the preview displays used here should give ample time for observers to set up multifocal attention in both tasks, and therefore the hemifield effect should be observed in both tasks. However, if spatial selection underlies the hemifield effect, then the hemifield effect should be observed in the subset condition of the current experiment, which requires spatial selection of the intermediate row of letters, but there should be no hemifield effect in the standard search condition, which does not require spatial selection.

Finally, in Experiments 1 and 2, observers were strongly encouraged to maintain fixation, but eye movements were not monitored. To eliminate any possible effects due to differences in eye-movement behavior, we monitored eye position in all of the remaining experiments (3A, 3B, 4) to ensure that observers maintained fixation throughout every trial.

Method

Participants

Nine naïve observers gave informed consent, had normal or corrected-to normal vision, and were paid or received course credit for their participation.

Stimuli

The stimuli for the subset search task are shown in Figure 4. Each display consisted of letters within two quadrants and waffle-shaped masks on the vertical and horizontal midlines of those quadrants. The masks were present to increase the spatial selection demands of the subset search task. In each display, a black fixation cross $(1.2^{\circ} \times 1.2^{\circ})$ was always present, and the letters and masks subtending 1.2° × 1.2° appeared at three different eccentricities (2.5°, 5°, and 7.5°). Observers knew that the target would be contained within the middle eccentricity. At the beginning of each trial, mask placeholders appeared at all locations so that observers knew where the stimuli would appear on that trial. The placeholders could appear in a bilateral alignment (in either the upper or lower visual field) or in a unilateral alignment (in either the left or right visual field). The placeholders appeared for 1000 ms, after which segments of the placeholders disappeared to reveal letters, though placeholders on the vertical and horizontal meridians remained unchanged so that letters never appeared on the vertical or horizontal midlines. One search target, the letter T rotated either clockwise or counterclockwise by 90°, appeared within the second eccentricity. The inner and outer letters were distractor Ls randomly oriented 0°, 90°, 180°, or 270° from vertical or distractor Ts rotated either clockwise or counterclockwise by 90°. The irrelevant Ts in the inner and outer rings were intended to further encourage observers to spatially select the middle ring.

Participants also performed a standard visual search in which only the middle ring of letters was presented, without the inner and outer letters and without the masks on the midlines. The trial sequence consisted of pretrial mask placeholders so that observers knew where the search items would be, but there were no task irrelevant items or masks in the search display (see Figure 4).

Apparatus

Stimuli were presented on a 24-inch liquid crystal display monitor with a 60-Hz refresh rate. Eye position was monitored by a video-based, desk-mounted IScan (Woburn, MA) 18,937 eyetracker sampling at 60 Hz. The left eye was tracked. A chin and forehead rest was used to minimize head movement and to maintain a constant viewing distance of 57 cm. The experiment was controlled by a computer running MATLAB with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Gaze position samples were streamed in real time from the eyetracker to the computer running MATLAB. Gaze-position data was used to control trial events, such as terminating trials when a participant broke fixation. Manual responses were collected using a keyboard.

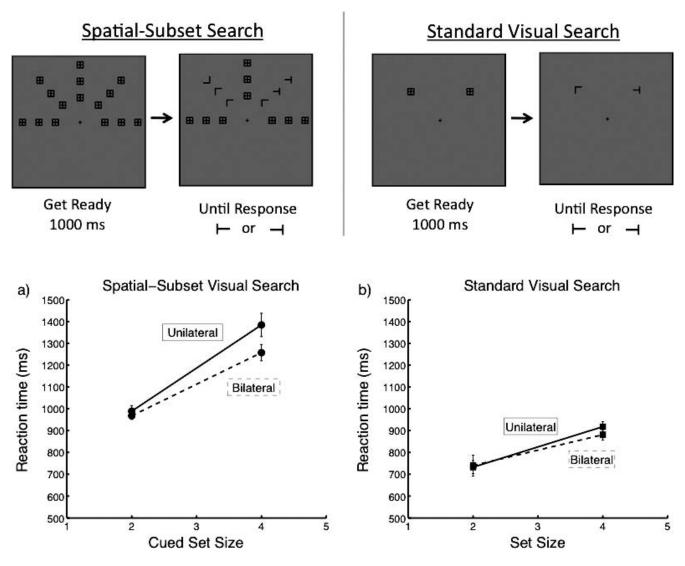


Figure 4. Displays and results of Experiment 3A. The top panel illustrates sample trials of the spatial subset search task and the standard search task. In the spatial subset search task, observers knew that the target would appear in the middle ring of the display. There were additional foil targets in the other rings to further encourage observers to focus on the middle ring. Placeholders also appeared on the midlines during the precue and test display in order to enhance the spatial-filtering demands. In the standard search, precues alerted the participant to the locations that would be task relevant, but no irrelevant items or placeholders were ever presented. The bottom panel shows reaction time (ms) versus set size for correct responses on each task. Error bars show within-subject standard error of the mean.

(a) In the spatial subset visual search task, reaction times are longer in the unilateral condition than in the bilateral condition, with a reliable difference emerging at set size 4. (b) In the standard visual search task, there was no difference between unilateral and bilateral displays.

Procedure

Participants pressed a key to initiate each block of trials. Each block began with an eyetracker calibration sequence where participants would be asked to direct their gaze to several circles on the screen as part of a calibration sequence. This calibration would be used for the subsequent block of trials. On each trial, the fixation cross appeared for 1000 ms, followed by placeholders for 1000 ms. Then, segments of the placeholders disappeared to reveal letters. The task was to find the T and report its orientation as quickly

and as accurately as possible. After a short practice block, participants completed 384 trials with two search tasks (subset search versus standard search), two set sizes (2 versus 4), and two hemifield alignments (bilateral versus unilateral) randomly mixed within the session.

Participants were instructed to focus their attention only on positions contained within the intermediate eccentricity and were informed that the target would appear only within this subset of items. Because target items appeared only at the intermediate eccentricity,

Set size	Spatial subset		Standard	
	Bilateral	Unilateral	Bilateral	Unilateral
2	3.6 (1.0)	1.9 (0.6)	4.8 (0.8)	1.8 (1.3)
4	3.9 (1.1)	2.9 (0.9)	3.0 (1.0)	1.3 (0.9)
Average	3.8 (0.9)	2.4 (0.6)	3.9 (0.6)	1.5 (1.0)

Table 3. Error rate for each condition in Experiment 3A.

there was no need to cue participants to the location of the relevant items, and so there was no working memory load in this task. Thus, participants were required to maintain a top-down attentional filter, focusing their attention on the relevant locations and ignoring the irrelevant locations. Participants were also asked to maintain fixation throughout each trial. If participants shifted their gaze greater than 1° away from the fixation cross, the trial would be terminated and participants would be presented with a new trial of the same trial type.

Results

Participants rarely moved their eyes away from fixation during a trial (7% of the time), and were equally likely to do so in the bilateral and unilateral condition (7.5% and 6.4%, respectively; t[8] = 0.83, p = 0.43, $r^2 = .08$). Trials in which participants broke fixation were terminated and not included in subsequent analyses.

Overall error rates were low (bilateral versus unilateral, 2% and 4%, respectively, see Appendix, and Table 3), and the following analysis focuses on reaction time for trials in which participants responded correctly.

As shown in Figure 4, there was a reliable hemifield effect (bilateral reaction time was faster than unilateral reaction time) in the spatial subset search task that emerged as set size increased (Figure 4a). In contrast, there was no effect of hemifield alignment in the standard search task (Figure 4b).

A three-way ANOVA was run on reaction time with search task (subset versus standard), set size (2, 4), and hemifield (bilateral versus unilateral) as factors. There was a main effect of hemifield (F[1,8] = 6.7, p = 0.03, $\eta^2 = .46$), but the interaction between task and hemifield was not reliable (F[1,8] = 2.0, p = 0.19, $\eta^2 = .20$). Based on the results of Experiments 1 and 2, we expected there to be a hemifield effect only at higher set sizes of the spatial subset search task. Thus, we also conducted planned, focused analyses to test these predictions.

A two-way ANOVA was run on reaction time for the subset search task with set size (2, 4) and hemifield alignment (bilateral versus unilateral) as factors. Reaction times were slower at the largest set size $(F[1,8] = 59.386, p < 0.001, \eta^2 = .881)$, again indicating

that there was a cost to having a larger set of possible target locations. Most importantly, there was a main effect of hemifield alignment (F[1,8]=7.476, p=0.026, $\eta^2=.483$), indicating that reaction time was significantly slower in the unilateral condition than in the bilateral condition. Focused *t*-tests comparing reaction times in the bilateral versus unilateral alignment at set size 2 (t[8]=0.915, p=0.387, $r^2=.095$) and set size 4 (t[8]=2.687, p=0.028, t=0.028, t=0.

A two-way ANOVA was run on reaction time for the standard search task with set size (2, 4) and hemifield alignment (bilateral versus unilateral) as factors. As expected, reaction times were slower at the largest set size $(F[1,8] = 17.99, p < 0.01, \eta^2 = .692)$, indicating that there was a cost to having a larger set of possible target locations. Most importantly, there was no main effect of hemifield alignment (F[1,8] = 0.314, p= 0.591, η^2 = .038), indicating that a hemifield effect was not found or was greatly attenuated when irrelevant items were not present. Focused t-tests were performed to compare reaction times in the bilateral versus unilateral alignment at set size 2 (t[8] = 0.210, p = $0.839, r^2 = .005$) and set size $4(t[8] = 1.38, p = 0.204, r^2 = 0.005)$.193), confirming that a hemifield effect was not present at either set size.

Experiment 3B: Controlling for eye movements in feature subset search

Experiment 3B used the same procedure as Experiment 3A except that the task-relevant items were always white, while task-irrelevant items in the subset search task were black. Thus, the targets could be selected based on this salient feature difference. The results were expected to replicate those of Experiment 2, showing no difference between bilateral and unilateral displays in either standard visual search or feature subset search.

Method

Participants

Participants were 9 naïve observers who gave informed consent, had normal or corrected-to normal vision, and were paid or received course credit.

Stimuli

As shown in Figure 5, displays were identical to those in Experiment 3A except that the fixation point was white

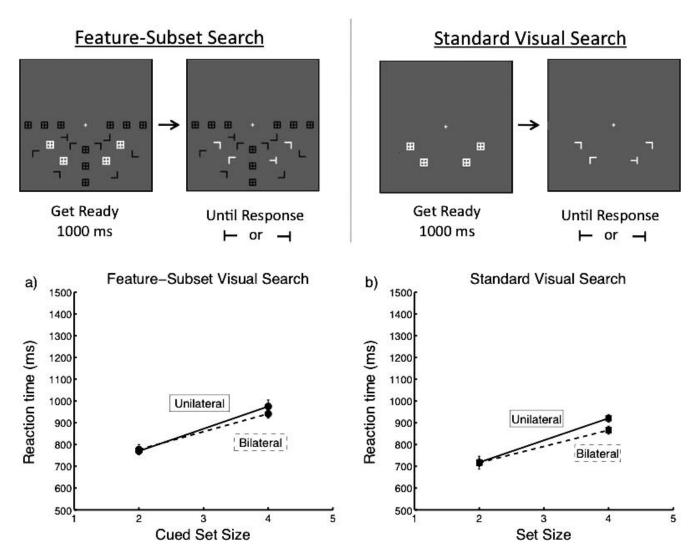


Figure 5. Displays and results of Experiment 3B. The top panel illustrates sample trials of the feature subset task and the standard search task. The displays were identical to Experiment 3A except that the task-relevant items were always white. The bottom panel shows reaction time (ms) versus set size for correct responses on each task. Error bars show within-subject standard error of the mean. (a) In the feature subset visual search task there was no reliable difference between unilateral and bilateral displays. (b) In the standard visual search task, there also was no reliable difference between unilateral and bilateral displays.

and the relevant subset of items was white throughout subset search trials. All pretrial placeholders and items were white throughout standard search trials.

Procedure

The procedure was identical to that of Experiment 3A.

Results

Participants rarely moved their eyes away from fixation during a trial (2% of trials) and were equally likely to do so in the bilateral and unilateral condition (2% and 3%, respectively; t[8] = 2.14, p = 0.065, $r^2 = .36$).

Overall error rates were low (bilateral versus unilateral, 3% and 1%, respectively; see Appendix, and Table 4), and the following analysis focuses on reaction time for trials in which participants responded correctly.

As shown in Figure 5, there was no reliable hemifield effect in either the standard or subset search task. For both the feature subset search (Figure 5a) and the standard visual search (Figure 5b), reaction time was nearly identical in the bilateral and unilateral conditions for both set size 2 and set size 4.

A three-way ANOVA was run on reaction time with search task (subset versus standard), set size (2, 4), and hemifield (bilateral versus unilateral) as factors. There was no main effect of hemifield $(F[1,8] = 1.56, p = 0.25, \eta^2 = .16)$, and the interaction between task and hemifield was not significant $(F < 1, p = 0.41, \eta^2 = 0.41, \eta^2$

Set size	Feature subset		Standard	
	Bilateral	Unilateral	Bilateral	Unilateral
2	3.7 (1.5)	1.2 (0.4)	3.9 (1.0)	0.7 (0.3)
4	1.9 (0.7)	1.6 (0.6)	2.8 (1.3)	1.2 (0.5)
Average	2.8 (0.9)	1.4 (0.3)	3.4 (1.0)	0.9 (0.4)

Table 4. Error rate for each condition in Experiment 3B.

.09). For comparison with Experiment 3A, we also conducted planned, focused analyses on each condition independently.

A two-way ANOVA was run on reaction time for the subset search task with set size (2, 4) and hemifield alignment (bilateral versus unilateral) as factors. Reaction times were slower at the largest set size $(F[1,8] = 30.445, p = 0.001, \eta^2 = .792)$, again indicating that there was a cost to having a larger set of possible target locations. Most importantly, there was no main effect of hemifield alignment $(F[1,8] = 0.452, p = 0.520, \eta^2 = .053)$. Focused *t*-tests comparing reaction times in the bilateral versus unilateral alignment at set size 2 $(t[8] = 0.289, p = 0.78, r^2 = .01)$ and set size 4 $(t[8] = 1.57, p = 0.154, r^2 = .24)$ revealed that there was no hemifield effect at either set size.

A two-way ANOVA was run on reaction time for the standard search task with set size (2, 4) and hemifield alignment (bilateral versus unilateral) as factors. As expected, reaction times were slower at the largest set size (F[1,8] = 31.0, p = 0.001, $\eta^2 = .795$), indicating that there was a cost to having a larger set of possible target locations. There was no main effect of hemifield alignment (F[1,8] = 2.6, p = 0.144, $\eta^2 = .247$), indicating that a hemifield effect was not found or was greatly attenuated when irrelevant items were not present. Focused t-tests were performed to compare reaction times in the bilateral versus unilateral alignment at set size 2 (t[8] = 0.088, p = 0.932, $t^2 = .001$) and set size 4 (t[8] = 1.975, t = 0.084, $t^2 = .328$), confirming that there was no reliable hemifield effect at either set size.

Discussion

The present experiment replicated the results of Experiments 1 and 2: search was significantly faster for displays divided between the left and right hemifields than for displays that were aligned entirely within a single hemifield, but only when a subset of items was selected based on location. There was no hemifield effect in the feature subset search or the standard search, even though there was ample time to set up multifocal attention during the preview display. Moreover, the hemifield effect in the spatial subset search was observed even though there were no spatial working memory demands in the current study,

because participants knew that the target would always appear within the intermediate ring of letters throughout the experiment. Finally, we can rule out a contribution from differential eye movements in the bilateral and unilateral displays because eye position was monitored and trials in which eye position deviated from fixation by more than 1° were terminated immediately and not included in the analysis. Overall, these results reinforce the conclusion that hemifield independence arises under conditions in which multifocal spatial selection is required.

The hemifield effect in Experiment 3A was not as large as in Experiment 1. This is likely due to the fact that the effect increases with set size, and we could not easily test set sizes greater than 4 along a single eccentricity without a high degree of self-crowding among the targets. Indeed, pilot data suggest that target—target crowding can also give rise to hemifield independence, even when there are no irrelevant items to suppress (see also the results of Experiments 1 and 2, standard search, highest set size). This suggests that hemifield independence might arise whenever spatial selection is required, whether due to the need to filter out task-irrelevant items or the need to prevent crowding among task-relevant items.

Experiment 4: General task difficulty does not drive hemifield independence

In Experiments 1, 2, and 3, only tasks that require spatial selection appeared to give rise to a hemifield effect in visual search. However, the spatial subset search was also consistently the most difficult search task with the slowest reaction times, suggesting the possibility that task difficulty drives the hemifield effect. On this account, more difficult tasks are more likely to give rise to independent processing between the hemifields. Indeed, this proposal has been made using a variety of perceptual matching tasks (Belger & Banich, 1992). To test this possibility for visual search, we had observers perform a standard visual search task in which there were no task-irrelevant items, but in which we manipulated task difficulty by varying target distractor similarity (Duncan & Humphreys, 1989). Figure 6 illustrates the easy search condition (identical to the standard search condition of Experiment 3) and the difficult search condition where the distractors were adjusted to appear more similar to the target. If task difficulty alone drives the hemifield effect, then a hemifield effect should emerge in the difficult search condition.

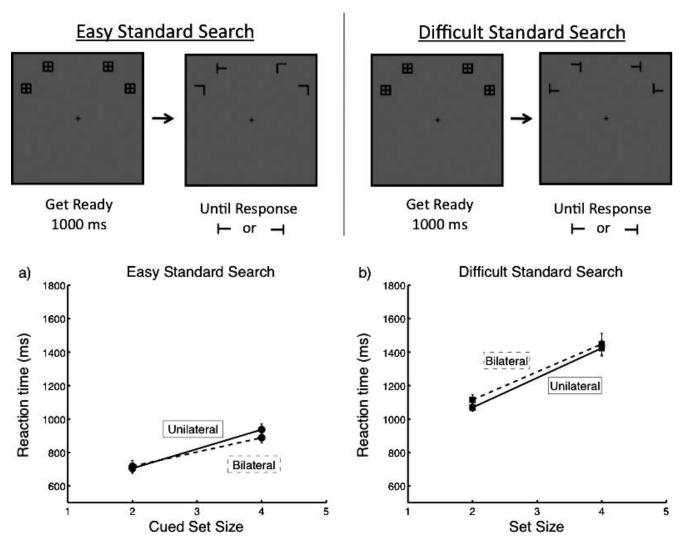


Figure 6. Displays and results of Experiment 4. The top panel illustrates sample trials of the easy and difficult search tasks. The easy search condition was the same as the standard search conditions of Experiments 3A and 3B. The difficult search displays were identical except that the line segments of the distractor Ls were offset to make them appear more similar to Ts. Both the easy search and difficult search conditions were standard search tasks in the sense that they did not have task-irrelevant items in the display. However, both tasks also had precues to alert observers to which locations would be relevant on a given trial. The bottom panel shows reaction time (ms) versus set size for correct responses on each task. Error bars show within-subject standard error of the mean. (a) In the easy search condition there was no overall effect of hemifield, although there was a significant interaction suggesting an increasing hemifield effect as set size increased (consistent with previous experiments). (b) In the difficult search task, although the numerical trend is towards faster reaction time in the unilateral condition, there was no main effect of hemifield (bilateral vs. unilateral) and no interaction between hemifield and set size.

Method

Participants

Fourteen naïve observers gave informed consent, had normal or corrected-to normal vision, and were paid or received course credit for their participation.

Stimuli

The stimuli for the easy search condition were the same as those for the standard search condition of Experiments 3A and 3B (see Figure 6). The only change

in the difficult search condition was that the distractor Ls had small offsets to make them look more like Ts (see Figure 6).

Procedure

In a pilot study we found that randomly mixing the easy search with the difficult search slowed performance in the easy condition (relative to the identical standard search condition of Experiments 3A and 3B). Thus, in the current study, conditions were blocked and

	Easy search		Difficult search	
Set size	Bilateral	Unilateral	Bilateral	Unilateral
2	5.4 (1.7)	2.8 (0.8)	15.5 (2.9)	15.8 (2.2)
4	3.1 (1.3)	4.0 (1.3)	29.6 (3.7)	27.5 (2.6)
Average	4.2 (1.4)	3.4 (0.8)	22.6 (2.7)	21.7 (2.0)

Table 5. Error rate for each condition in Experiment 4.

counterbalanced across observers. To familiarize observers with the conditions and task, each observer first performed 32 trials with easy search and difficult search trials randomly mixed. Then each observer completed 4 blocks of 96 test trials (2 blocks of the easy search condition, 2 blocks of the difficult search condition), with the order of conditions counterbalanced across subjects (ABBA, BAAB). Except for the blocking of conditions, the procedure was identical to that of Experiment 3, including the monitoring of eye position.

Results

Participants rarely moved their eyes away from fixation during a trial (7.3% of trials) and were equally likely to do so in the bilateral and unilateral conditions (7% and 8%, respectively; t[13] = 1.92, p = 0.08, $r^2 = .22$).

Overall error rates were low in the easy search condition and did not differ between the bilateral and unilateral displays (5% and 4%, respectively; t[13] = 1.41, p = 0.18, $r^2 = .13$). Error rates were higher in the difficult condition but also did not differ between bilateral and unilateral displays (25% and 23%, respectively; t < 1, p = 0.55, $r^2 = .03$). Appendix and Table 5 present error rates for each condition. The following analysis focuses on reaction time for trials in which participants responded correctly.

As shown in Figure 6, a hemifield effect did not emerge as task difficulty increased. In the easy search task, there was a trend for reaction time to be slower for the unilateral condition at set size 4 (Figure 6a), but for the difficult search task, the numerical difference was reversed, with faster reaction time in the unilateral condition than in the bilateral condition (Figure 6b).

A three-way ANOVA was run on reaction time with task (easy, hard), hemifield (bilateral, unilateral), and set size (2,4) as factors. The results showed that there was a large, robust main effect of task (F[1,13] = 56.9, p < 0.001, $\eta^2 = .814$) and set size (F[1,13] = 95.5, p < 0.001, $\eta^2 = .880$) but no significant effect of hemifield (F[1,13] = 0.0663, $I_0^2 = 0.015$). Most importantly, the interaction between task and hemifield was not significant (I[1,13] = 0.12, I[1,13] = 0.169, I[1,13] = 0.169,

Given that the specific hypothesis of interest was whether a reliable hemifield effect emerges as task difficulty increases, we also performed focused two-way ANOVAs on each task independently, with set size (2, 4) and hemifield (bilateral versus unilateral) as factors. In the easy search condition, there was no main effect of hemifield (F[1,13]=3.01, p=0.106, $\eta^2=.188$), but there was a small, reliable interaction between set size and hemifield (F[1,13]=5.39, p=0.037, $\eta^2=.293$). However, in the difficult search condition there was no effect of hemifield (F<1, p=0.346, $\eta^2=.069$) and no set size by hemifield interaction (F<1, p=0.573, $\eta^2=.025$). Thus, it does not appear that a robust hemifield effect emerges as task difficulty increases.

Discussion

The present experiment rules out the possibility that the hemifield effect is a consequence of task difficulty. Reaction time in the difficult search condition spans the range of reaction times where we observed the largest hemifield effect in the spatial subset search conditions of the previous experiments (1000-1200 ms in Experiment 1, 1200–1400 in Experiment 3A). Nevertheless, the difficult search condition of the present experiment does not show a hemifield effect at any set size. In fact, the numerical trend is in the opposite direction, with faster reaction times in the unilateral condition. Moreover, across all of our experiments, we found little evidence that task difficulty corresponds to the magnitude of the hemifield effect. To quantify this, we computed the size of the hemifield effect for all conditions across all experiments, excluding the spatial subset search conditions. This yielded 25 pairs of data points (bilateral versus unilateral trials at each set size for each task) for which we could estimate task difficulty by taking the mean reaction time, and the hemifield effect size using Cohen's D (the difference between means divided by their average variance). Overall, there was no correlation between reaction time and the hemifield effect ($r^2 = .002$). Combined, these findings suggest that increasing task difficulty alone does not give rise to a hemifield effect. Thus, the hemifield effect observed in the spatial subset search conditions of Experiments 1 and 3A does not appear to be caused by their general difficulty, providing further support for the conclusion that the critical factor is the requirement to spatially filter task-irrelevant items.

General discussion

Previous behavioral studies have revealed that attention can select targets independently in the left and right visual hemifields during an attentive tracking task (Alvarez & Cavanagh, 2005). However, this degree

of hemifield independence is not observed in other attentionally demanding tasks, such as visual search (Luck et al., 1989), suggesting that it may be specific to attentive tracking or attending to moving objects. Contrary to this possibility, the results of the current study showed a bilateral display advantage in a visual search task with stationary stimuli. This hemifield effect increased with the number of items selected and was observed only when items were selected based on location information but not when they were selected based on a salient feature difference, suggesting that hemifield independence is a signature of multifocal spatial selection.

Multifocal attention within versus across hemifields

Multifocal attention is the ability to attend to multiple objects without attending to regions between those attended objects (Cavanagh & Alvarez, 2005; McMains & Somers, 2004; Niebergall, Khayat, Treue, & Martinez-Trujillo, 2011). Previous findings suggest that multifocal attention is engaged when irrelevant distractor information must be suppressed. For instance, Awh and Pashler (2000) required observers to identify two targets at two spatially cued locations. Occasionally the cues were invalid, and targets would appear at two uncued locations, one that was in between the two cued locations and one that was not. If attention is split, then target detection should be no better at the uncued location that happens to be between the two cued locations than it would be at the more distant uncued location. Awh and Pashler (2000) found evidence that attention could be split into multiple foci more easily across the left and right hemifields than within a single hemifield, and that this splitting of attention depended on the presence of irrelevant distracting information. This suggests that multifocal attention is engaged when the suppression of task-irrelevant information is required. Similarly, other research has shown that there is a bilateral visual field advantage on elementary visual tasks, such as orientation discrimination or detection, but only when taskirrelevant distractors are present and have to be suppressed (Reardon, Kelly, & Matthews, 2009). These previous findings are consistent with the current results, suggesting that maintaining multiple independent foci of attention can be done more effectively in separate hemifields. Critically, the targets in these previous studies were selected based on location information. The results of the current study suggest that bilateral advantages on these tasks could be reduced or eliminated if the targets are selected based on a salient feature difference (e.g., color or luminance) rather than on location information.

Relationship to neural models of attention

The present study provides behavioral evidence that spatial attention is constrained by the locations of items in the visual field, whereas feature-based attention is not. We have argued that purely cognitive models cannot easily account for such findings without taking anatomical constraints into account. Here we discuss the relationship between the present findings and research on the neural basis of attention. Our goal is not to propose a specific neural model, but only to describe how the present findings fit with our current understanding of the neural basis of attention. Hopefully this provides a foundation for modifying cognitive and neural models to account for the present findings.

Maunsell and Treue (2006) have sketched out a framework for understanding the neural mechanisms of location-based and feature-based attention, with an emphasis on how attention modulates the firing rate of neurons (response gain). In this framework, when attention is directed to a location, it increases the response gain for any neuron with a receptive field that overlaps the attended location (e.g., McAdams & Maunsell, 1999; Moran & Desimone, 1985; Reynolds, Pasternak, & Desimone, 2000). In contrast, featurebased attention changes the response gain across the entire retinotopic map, with increased gain for neurons tuned to the task-relevant feature and decreased gain for neurons that are not tuned to the task-relevant feature (e.g., Bichot, Rossi, & Desimone, 2005; Martinez-Trujillo & Treue, 2004).

Within this framework, hemifield effects on attention might emerge at either the level of attentional control or the site of attentional modulation. For example, location-based attention might have independent control mechanisms for directing attention to locations in the left and right visual fields, whereas feature-based attentional control might be a unified process designed to broadcast feature preferences across the entire visual field. Consistent with this possibility, location-based parietal functions are strongly dependent on ipsilateral connections to lower level areas whereas feature-based temporal functions appear to depend equally on ipsilateral and contralateral connections (Mishkin & Ungerleider, 1982). Thus, it is possible that locationbased attention relies on parietal mechanisms with strong ipsilateral connections to lower level areas and that feature-based attention relies on temporal lobe mechanisms with balanced ipsilateral and contralateral connections.

Alternatively, the hemifield effect might not depend on attentional control mechanisms, but instead on interactions at the site of attentional modulation (Scalf & Beck, 2010). For example, it appears that spatial attention enhances responses at the attended location and suppresses responses to surrounding locations (Muller & Kleinschmidt, 2004; Muller, Mollenhauer,

Rosler, & Kleinschmidt, 2005; Niebergall et al., 2011). This suppression could give rise to hemifield effects if suppression depends on lateral connections that are stronger within a region than across regions, since many lower level visual areas have separate hemifield representations (V1, V2, V3, lateral occipital area [LO], V7, MT: Gardner, Merriam, Movshon, & Heeger, 2008; V6: Pitzalis et al., 2006; V8: Hadjikhani, Liu, Dale, Cavanagh, & Tootell, 1998). For example, right V1 has a representation of the left visual field, whereas left V1 has a representation of the right visual field. If suppressive effects spread more strongly within a region, then attending to a target in the left visual field will increase right V1 response at that location but will suppress right V1 response at neighboring locations (i.e., at other locations in the left visual field).

Although the majority of research on the neural mechanisms of attention focuses on how attention modulates firing rates, recent research has turned the focus to how attention decorrelates the firing of neurons (Cohen & Maunsell, 2011; Mitchell, Sundberg, & Reynolds, 2009). If neurons fire together, then their signals are redundant and therefore less informative. Thus, decorrelating the firing of neurons can increase the amount of independent information in the population. Both location-based attention and feature-based attention reduce the correlation in firing rate between neighboring neurons (Cohen & Maunsell, 2011). However, feature-based attention was found to be coordinated across the hemifields, whereas locationbased attention was found to be independent across the hemifields (Cohen & Maunsell, 2011). Thus, spatial attention appears to operate over local groups of neurons within a hemisphere, whereas feature-based attention appears to operate over larger groups across hemispheres. This pattern is consistent with the behavioral results reported here and reinforces the conclusion that spatial attention can operate independently across hemifields.

Anatomical constraints on attentional selection

Attention is the mechanism that selects some perceptual inputs and gives them priority for processing and representation over other perceptual inputs. Perhaps the most basic question we can ask about attention is what the units of selection are. Cognitive theories of attention have focused on candidate units such as spatial locations (Eriksen & St. James, 1986; Eriksen & Yeh, 1985; Helmholtz, 1962), basic visual features (Kumada, 2001; Rossi & Paradiso, 1995; Saenz, Buracas, & Boynton, 2003), segmented regions and surfaces (Ben-Shahar, Scholl, & Zucker, 2007; He & Nakayama, 1992, 1995), and objects (Duncan, 1984; O'Craven, Downing, & Kanwisher, 1999; Scholl, Pyly-

shyn, & Feldman, 2001). The current results complement this cognitive approach by emphasizing that the units of selection are represented within a neural system, and the architecture of this system will impose an important constraint on attentional selection. Thus, a complete understanding of the units selected by attention will require an understanding of the neural representation of locations, features, surfaces, and objects.

While visual attention is a high-level process, the mechanisms of selection operate over a neural representation of the visual world. Thus, it seems likely that the architecture of the visual system will impose an important constraint on attentional selection. The current studies show that location-based attentional selection shows a strong bilateral visual field advantage, with faster processing of information that is divided between hemifields than information presented within a single hemifield, whereas feature-based attentional selection shows no such advantage. The operation of location-based attention appears to be limited by a representation in which the hemifields are represented separately, which includes many visual areas in humans (V1, V2, V3, LO, V7, MT: Gardner et al., 2008; V6: Pitzalis et al., 2006; V8: Hadjikhani et al., 1998). Moreover, the network of areas believed to provide the neural basis of the saliency map for attentional selection (Fecteau & Munoz, 2006) has also been shown to respond mostly to stimuli in the contralateral hemifield in humans: the frontal eye fields (Hagler & Sereno, 2006), the putative human lateral intraparietal cortex (LIP; Sereno, Pitzalis, & Martinez, 2001), the superior colliculus (Schneider & Kastner, 2005), and the pulvinar (Cotton & Smith, 2007). In contrast, featurebased selection operates over an integrated, higher level representation of the visual world, which could be associated with higher level object recognition areas that show feature maps (e.g., inferior temporal cortex [IT], lateral occipital complex [LOC], and the fusiform face area [FFA]). Indeed, substantial bilateral responses are observed mostly in higher level object recognition areas such as the lateral occipital area and fusiform face area (Hemond, Kanwisher, & Op de Beeck, 2007). Future work will be necessary to determine whether this is a universal characteristic of feature-based selection by requiring selection on different basic visual features (e.g., motion, orientation) or visual categories (e.g., faces or houses). More generally, theories of visual attention should take into account the important role of visual anatomy in visual selection.

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Footnote

¹ Search is often modeled as a strictly serial process (Treisman & Gelade, 1980; Wolfe, Cave, & Franzel, 1989) in which there is only a single focus of attention. Other models propose a massively parallel process that operates over all items simultaneously but is imperfect and noisy, resulting in set size effects (Eckstein, Thomas, Palmer, & Shimozaki, 2000). In some cases, a handful of items are assumed to be processed in parallel (Pashler, 1987), but the selection is modeled as a single focus encompassing several items in clumps rather than multiple independent foci, as has been proposed for multiple-object tracking (Cavanagh & Alvarez, 2005; Intriligator & Cavanagh, 2001; Pylyshyn & Storm, 1988).

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Appendix

Our primary analyses focus on reaction time for correct trials. However, it is important to ensure that differences in reaction time patterns are not due to differences in tradeoffs between speed and accuracy. For example, if one task shows a bilateral advantage (faster reaction time for bilateral displays) and another task does not, then it is important to make sure that observers are not just sacrificing accuracy in the bilateral condition of the task that does show an effect. The tables show that overall reaction times are very low across all conditions of all experiments, with the exception of the difficult search condition of Experiment 4. While there is a consistent trend for higher error rates in the bilateral condition across all experiments and tasks, any differences between bilateral and unilateral accuracy rates are very small (typically 1–2%) and usually not reliably different (see Results section for each experiment). More importantly, this trend is comparable across all tasks, suggesting that it does not drive the hemifield effect (this trend is present in most tasks, but most tasks do not show a hemifield effect). Indeed, the feature subset search of Experiment 2 shows one of the largest differences in error rates for the bilateral and unilateral condition and yet shows no hemifield effect in reaction time. Thus, our hemifield effects in reaction time do not appear to be due to speed–accuracy tradeoffs.