# Beyond Capacity: The Importance of Attentional Coordination

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Beyond Capacity:  
The Importance of Attentional Coordination

A dissertation presented  
by  
Roger W. Strong  
to  
The Department of Psychology

in partial fulfillment of the requirements  
for the degree of  
Doctor of Philosophy  
in the subject of  
Psychology

Harvard University  
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Beyond Capacity: The Importance of Attentional Coordination

Abstract

Visual attention is the process of prioritizing visual information relevant to current behavioral goals (e.g., prioritizing cars over billboards while driving). A large body of research has characterized various attentional systems, while additionally exploring whether the capacity of those systems can be improved with training. Despite this work, training paradigms attempting to increase attentional capacity have largely failed to produce benefits that generalize from trained tasks to untrained tasks. The research presented in this dissertation demonstrates that attentional processing is limited not only by the capacity of individual cognitive systems, but also by the ability of those systems to coordinate with one another. In the first chapter, an attentional training study demonstrates that rather than enhancing the general capacity of attentional control, training may instead enhance the coordination between attentional control systems and task-specific representations. In the second chapter, behavioral studies demonstrate that separate control of spatial attention exists for the left and right visual hemifields, indicating that coordination between these hemifield-specific control systems is necessary for completing spatial attention tasks. Finally, the third chapter shows that hemifield-specific attentional control systems exchange information when attended information moves between hemifields, and that the efficiency of this exchange depends on how attention is allocated. Because attention is limited by interactions between separate cognitive systems, cognitive training studies should explore whether enhancing these interactions can produce generalized training benefits.
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General Introduction

The Importance of Attention

In everyday life, we prioritize our time and resources. We cannot be in multiple locations at once, share an equal amount of time with each of our friends and family members, or spend all of our money on travel. Similarly, the human visual processing system cannot give equal priority to everything it encounters, and must instead prioritize information relevant to current behavioral goals, a process called attention. The importance of attentional processing is especially salient in populations with disordered attention; for example, hemispatial neglect patients lose the ability to perceive half their world due to faulty attentional processing (Posner, Walker, Friedrich, & Rafal, 1984). Even for healthy individuals, attentional processing is critical for performing many everyday tasks (e.g., prioritizing cars over billboards while driving) and is correlated with measures of intelligence (Oksama & Hyönä, 2004; Tullo, Faubert, & Bertone, 2018; Wilmer, Martini, Germine, & Nakayama, 2016), highlighting its importance to human cognition.

Attentional Capacity and Training

Given the importance of attention, it is unsurprising that a great deal of research has characterized various subcomponents of attentional processing (Knudsen, 2007; Posner & Petersen, 1990) and their limits (Pylyshyn & Storm, 1988; Rensink, O’Regan, & Clark, 1997; Simons & Chabris, 1999). Despite the vast amount that has been learned about attentional processing through this work, training paradigms attempting to increase attentional capacity have largely failed to produce benefits that generalize from trained tasks to untrained tasks (Allaire et al., 2014; Simons et al., 2016). To produce generalized training benefits, training paradigms must
enhance cognitive processes used during untrained tasks (Ahissar & Hochstein, 2004). Therefore, training paradigms often use training and outcome measures that likely depend on common cognitive processes (e.g., multiple-object tracking and soccer, which are both thought to rely on spatial attention; Romeas, Guidner, & Faubert, 2016), hoping that improved performance on training tasks will generalize to outcome measures due to a shared cognitive capacity.

The possibility of generalized training benefits is plausible given that a common network of brain regions has been implicated across a variety of attention and executive functioning tasks, including tasks associated with intelligence (Duncan, 2006; Duncan, 2010; Duncan & Owen, 2000). Enhancing this network could increase the capacity of a general attentional “spotlight” (Norman, 1968; Posner, Snyder, & Davidson, 1980), allowing training benefits to generalize to untrained tasks limited by the same capacity as the training task. However, this strategy for producing generalized training benefits relies on two potentially incorrect assumptions: 1) that attentional processing is limited primarily by the capacity of a general attentional spotlight, and 2) that the capacity of this spotlight can be enhanced with training.

*Debate Over Multiple Attentional Spotlights*

Is attention limited primarily by the capacity of a general attentional spotlight? Although we typically experience a single awareness of the world, the behavior of split-brain individuals (i.e., individuals with a severed corpus callosum) has revealed the ability of the cerebral hemispheres to operate separately from one another. For example, split-brain patients complete visual search tasks faster when both hemispheres can contribute to information processing during bilateral stimulus presentations (e.g., four items in the left visual hemifield, four items in the right visual hemifield), compared to when processing is restricted to only 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 was not found for healthy individuals 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 half of the visual field. Although a dissociation was found between split-brain and healthy individuals for Luck et al.’s visual search task, more recently a bilateral field advantage has been found in healthy observers across a variety of tasks (Delvenne, 2012), most notably when tracking moving targets with attention (where healthy observers can track twice as many targets successfully when the targets are divided between the hemifields; Alvarez & Cavanagh, 2005). This result suggests that separate attentional control over each hemifield may not be a unique consequence of severing the connections between the two cerebral hemispheres, but instead be a standard feature of visual processing.

Although consistent with separate control of attention for each hemifield, the bilateral field advantage in healthy individuals can also be accounted for by a single attentional spotlight, which is limited by hemifield-specific spatial interference at early stages of visual processing (Franconeri, Jonathan, & Scimeca, 2010; Störmer, Alvarez, & Cavanagh, 2014). Because the bilateral field advantage is consistent with both A) separate spotlights of attention for each hemifield, and B) a single attentional spotlight limited by spatial interference, it remains unclear whether healthy individuals have separate control of attention in each hemifield. Differentiating between accounts of a single spotlight versus multiple spotlights is important when considering the possibility of enhancing attentional processing, as the existence of separate attentional spotlights would indicate that attention is limited not only by a general capacity, but also by the interaction of separate attentional components.
Plan of Dissertation

This dissertation provides evidence that attentional processing is limited not only by the general capacity of individual cognitive systems, but also by the ability of those systems to interact with one another. Each chapter demonstrates this point using the multiple-object tracking paradigm, which requires observers to distinguish moving targets from distractors (which are identical to the targets other than their spatial location; Cavanagh & Alvarez, 2005; Pylyshyn & Storm, 1988). Multiple-object tracking is a useful paradigm for studying attention, as it is a task limited primarily by attention (and not lower-level representational constraints; Alvarez & Franconeri, 2007). For example, observers rarely have trouble differentiating individual objects when completing multiple-object tracking tasks; instead the challenge is using attention to maintain which objects are targets and which are distractors. Additionally, multiple-object tracking has previously been used in studies assessing the two main topics addressed in this dissertation: 1) the generalization of cognitive training benefits (Green & Bavelier, 2006; Romeas et al. 2016; Thompson et al., 2013), and 2) the possibility of hemifield-specific attentional spotlights (Alvarez & Cavanagh, 2005; Franconeri et al., 2010; Störmer, et al., 2014).

The first chapter of this dissertation explores whether a shared attentional capacity between trained and untrained tasks is sufficient for achieving generalized training benefits. Despite both training and outcome measures being multiple-object tracking tasks limited by a common attentional capacity, training benefits showed very limited generalization to the untrained tasks. This extreme specificity of training benefits demonstrates that rather than enhancing the general capacity of attentional control, training may instead enhance coordination between systems for attentional control and systems for representing task-specific information. Therefore, a shared capacity between training and outcome measures is insufficient for
producing generalization.

The second chapter investigates whether separate control of spatial attention and working memory exists for the left and right visual hemifields. Although evidence consistent with hemifield-specific processing has previously been documented (Alvarez & Cavanagh, 2005; Delvenne, 2005), these results can also be explained by single attentional capacity functioning more effectively when information is divided between hemifields (versus contained within a single hemifield; Franconeri, et al., 2010; Störmer et al., 2014). In the experiments presented in Chapter 2, observers had difficulty maintaining targets that crossed between the hemifields with attention and working memory, a finding consistent with hemifield-specific control of attention and incompatible with a single attentional spotlight. This evidence for separate control over each hemifield indicates that coordination between hemifield-specific spotlights is necessary for completing tasks that require spatial attention.

Finally, the third chapter demonstrates that hemifield-limited attentional systems exchange their information with one another as targets move between the hemifields, and that the effectiveness of this exchange depends on whether attention is divided between the hemifields or allocated to a single hemifield. These findings again highlight that attentional processing is limited by the ability of separate attentional systems to interact with one another, while additionally demonstrating that the efficiency of this interaction differs during focal and divided attention.

Together, these studies demonstrate that attentional processing is limited not only by the capacities of individual attentional control systems, but additionally by both A) coordination between attentional control systems and representational systems (Chapter 1), and B) coordination between separate attentional control systems for each hemifield (Chapters 2 and 3).
These findings challenge an assumption underlying many cognitive training paradigms: that a shared cognitive capacity between training an outcome measures is sufficient for producing generalized training benefits. Additionally, these findings suggest a new avenue of exploration into achieving generalized training benefits: enhancing the coordination between separate high-level attentional systems, rather than attempting to enhance general attentional capacity.
Chapter 1

Training enhances attentional expertise, but not attentional capacity:
Evidence from content-specific training benefits.

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Abstract

Cognitive training has become a billion-dollar industry with the promise that exercising a cognitive faculty (e.g., attention) on simple “brain games” will lead to improvements on any task relying on the same faculty. While this logic seems sound, it assumes performance improves on training tasks because attention’s capacity has been enhanced. Alternatively, training may result in attentional expertise – an enhancement of the ability to deploy attention to particular content – such that improvement on training tasks is specific to the features of the training context. The present study supported this attentional expertise hypothesis, showing that training benefits did not generalize fully from a trained attentional tracking task to untrained tracking tasks requiring a common attentional capacity, but differing in seemingly superficial features (i.e., retinotopic location and/or motion type). This specificity suggests that attentional training benefits are linked to enhanced coordination between attentional processes and content-specific perceptual representations. Thus, these results indicate that shared attentional capacity between tasks is insufficient for producing generalized training benefits, and predict that generalization requires attentional expertise for content present in both training and outcome tasks.
Training enhances attentional expertise, but not attentional capacity: Evidence from content-specific training benefits.

Cognitive training is a billion-dollar industry (Fernandez, 2013), fueled by consumers striving to maximize their cognitive abilities. By improving performance on training tasks, customers seek benefits in everyday life, such as heightened awareness while driving or better memory for coworkers’ names. To produce such generalized benefits, practicing a training task must use and enhance mechanisms critical to untrained tasks (Ahissar & Hochstein, 2004). Therefore, training paradigms typically use training and outcome measures that putatively depend on common cognitive mechanisms (e.g., working memory tasks and fluid intelligence tasks; Jaeggi, Buschkuehl, Jonides, & Perrig, 2008), hoping that training will improve performance on untrained tasks by enhancing a core cognitive ability, such as attention or memory. Although the logic of strengthening cognitive abilities in one context for use in another seems sound, examples of generalized training benefits are limited, and when found (Green & Bavelier, 2003; Jaeggi et al., 2008) often cannot be reproduced (Murphy & Spencer, 2009; Thompson et al., 2013). This inconsistency has generated criticism of training programs: in 2014 75 cognitive scientists released a statement declaring that little evidence exists supporting the efficacy of cognitive training products (Allaire et al.), while in 2016 the cognitive training company Lumosity was fined $2 million for deceptive claims about the effectiveness of its products (Federal Trade Commission). This criticism highlights the need for a better understanding of the mechanisms enhanced by training.

In the present study, we trained participants on an attentional tracking task, then measured the degree of generalization to similar untrained tracking tasks that differed only in the features of the tracked items (translational vs. rotational movement, upper vs. lower visual field;
see Figure 1.1). This paradigm allowed us to differentiate between two possibilities for how training might enhance attentional processing, which we label the “capacity-enhancing” and “expertise-building” hypotheses of attentional training. The capacity-enhancing hypothesis is the motivation behind cognitive training paradigms which posit that training increases a general attentional capacity’s overall strength or effectiveness (e.g., Green & Bavelier, 2003). Analogous to how strength-training exercises (e.g., bench press) produce improved performance in untrained tasks that use the same muscles (e.g., lifting heavy furniture), the capacity-enhancing hypothesis predicts that improvement on training tasks should generalize to untrained tasks that use the same attentional capacity. In contrast, the expertise-building hypothesis posits that training does not improve general attentional capacities, but instead enhances the coordination between these capacities and task-specific representations (red line in Figure 1.1). In other words, the expertise-building hypothesis predicts that training allows an attentional capacity to make better use of training-specific representational content, without enhancing the capacity more generally. Analogous to how improving one skill requiring creativity (e.g., writing a poem) does not necessarily generalize to similar skills requiring creativity (e.g., writing a short story; Baer, 1996), the expertise-building hypothesis predicts that improvements on training tasks will fail to generalize to untrained tasks that do not require the attentional processing of content present during training, even when the trained and untrained tasks rely on the same attentional capacity (Figure 1.1).

We compared the predictions of the capacity-enhancing and expertise-building hypotheses by testing the transfer of training benefits between four very similar laboratory tasks (Figures 1.1 & 1.2). Each task is a variant of the multiple-object tracking paradigm (Cavanagh & Alvarez, 2005; Pylyshyn & Storm, 1988), which measures the ability to maintain attention
simultaneously on multiple moving targets. Because multiple-object tracking is limited primarily by attentional processing (Alvarez & Franconeri, 2007; although a pre-attentive indexing of individual items may be required, Pylyshyn & Storm, 1988), it is a likely candidate to show generalization of training benefits under the capacity-enhancing hypothesis. This characteristic has led to the use of tracking tasks across a variety of cognitive training experiments. When used as an outcome measure for assessing the efficacy of other training paradigms, improvements in tracking performance have been found following video game training (Green & Bavelier, 2006), but were not found following improvement on a working memory task (Thompson et al., 2013). Following the completion of certain tracking training paradigms, benefits such as improved soccer performance (Romeas, Guldner, & Faubert, 2015), better biological motion perception (Legault & Faubert, 2012), and the enhancement of various cognitive functions (Parsons et al., 2014) have been reported, although other studies have failed to find generalization from tracking improvement to measures of working memory performance (Arend & Zimmer, 2012; Thompson et al., 2013). Additionally, tracking ability has been associated with performance in expert populations such as radar operators (Allen, McGeorge, Pearson, & Milne, 2004), professional athletes (Faubert, 2013), and laparoscopic surgeons (Harenberg et al., 2016), making it an intriguing task for comparing the predictions of the capacity-enhancing and expertise-building hypotheses of attentional training.
Figure 1.1: Example Stimuli and Possible Training Outcomes. Target items blinked white before fading to black as items began to move on screen (indicated by arrows). All of the tasks are known to share attentional capacities (based on the dual task experiment reported in Appendix A1). The top panel shows general attentional mechanisms, and highlights “shifting attention” as a possible general capacity shared by the tracking tasks. The arrows show that this general capacity is deployed to each of the tracking tasks (rotational, translational, upper visual field, lower visual field). The capacity-enhancing hypothesis assumes that training enhances general attentional capacities (“shifting attention” in this example), and therefore predicts that improvement on the training task (e.g., tracking translating dots in the upper visual field) should generalize to the untrained tasks, which are limited by a common attentional capacity. In contrast, the expertise-building hypothesis predicts that general mechanisms (e.g., “shifting attention”) become more effectively deployed to representations specific to the training context (translational motion in the upper visual field in this example), and therefore predicts that improvement should be specific to the trained task (red arrow).

The four attentional tracking tasks used in the present study differed only in how the objects moved (translating dots versus rotating pinwheels) and where the objects were located in the visual field (upper versus lower visual field). Based on their similarity, it seems reasonable to assume that these tracking task share attentional resources. However, previous work has shown that two otherwise identical tracking tasks can draw on completely independent attentional
resources when presented in separate hemifields (Alvarez & Cavanagh, 2005). Thus, in order to ensure that these tasks are attentionally demanding and share common attentional resources, we ran a preliminary experiment using a dual-task method (the attentional operating characteristic, Sperling & Melchner, 1978; see Appendix A1). The results of this experiment showed that completing any pair of the tracking tasks simultaneously resulted in a direct performance tradeoff between the tasks (i.e., participants had to perform worse on one task to do better on the second), unlike tasks that draw from independent capacities (tracking in the left vs. right hemifield; Alvarez & Cavanagh, 2005) or partially independent capacities (tracking vs. search; Alvarez, Horowitz, Arsenio, DiMase, & Wolfe, 2005). Thus, these preliminary results show that all the tracking tasks used in our training study are limited by a common attentional capacity (or possibly multiple common capacities critical to tracking, such as the capacities for shifting attention and sustaining attention). Therefore, any improvement in the trained task that is the result of an enhanced attentional capacity would generalize to the other tasks.

Having established that the four attentional tracking tasks in the present study are limited by a common attentional capacity (or multiple common capacities), we trained participants using either the translating dots or the rotating pinwheels motion type, and compared their performance to a no-training control group to account for practice effects. If training enhances attentional capacity (capacity-enhancing hypothesis), we expect complete generalization between the four tracking tasks, as each shares an attentional capacity critical to tracking performance. However, although we verified that these four tasks are limited by a common attentional capacity, each uses different representational mechanisms specific to translational versus rotational motion (Morrone et al., 2000) and to the representation of the upper versus lower visual field (Holmes & Lister, 1916; Sereno et al., 1995). Thus, if training enhances attention’s coordination with
content-specific representations (expertise-building hypothesis), we expect improvement to be specific to the training context (i.e., to the location and type of motion practiced during training).

**Figure 1.2**: Training Design. After pre-training assessment, participants trained for 6 days on one multiple-object tracking motion type in one location before completing a post-training assessment (training on dot tracking in the upper left quadrant shown here, but counterbalanced across location and motion type). Control subjects completed same training design, except for taking days 3-8 off instead of training.

**Method**

**Procedure**

Over a 10-day training design (Figure 1.2), participants were required to track moving objects with their attention while keeping their eyes focused on a central fixation point (Figure 1.1). Following an initial practice day, pre-training speed thresholds were determined for four different tracking tasks (translating dots and rotating pinwheels, in the upper and lower visual fields). Participants next completed 6 days of training, practicing one motion type in one retinotopic location (e.g., translating dots in the top left quadrant). Following the training period, post-training speed thresholds were determined for the four tracking tasks. This design allowed analysis of whether performance benefits for the trained motion type in the trained retinotopic
location (trained condition) generalized to the untrained motion type in the trained location (new motion condition), the trained motion type in the untrained location (new location condition), or the untrained motion type in the untrained location (both new condition).

On day one of the experiment, participants completed approximately 30 minutes of practice trials, containing a mix of the two motion types in either the upper-left and lower-left or the upper-right and lower-right visual quadrants. Participants were required to take a short break 15 minutes into this practice session. On day two of the experiment, pre-training tracking speed thresholds were obtained for both motion types (translating dots and rotating pinwheels) in two retinotopic locations (the upper and lower visual field on the opposite left/right side of the screen from the practice day). Two randomly interleaved staircases were completed (10 reversals – see Appendix A2 for full description of staircase parameters) for each of the four multiple-object tracking motion type/location combinations (resulting in eight total staircases being completed). For each staircase, we estimated the speed threshold by averaging the final four reversal speeds, resulting in two speed-threshold estimates per motion type/location combination; the mean of these two speed-thresholds was used as the baseline speed for each motion type/location combination. Participants were required to take a short break every 20 minutes until all staircases were completed.

For days 3-8, participants completed approximately 55 minutes of trials of one motion type in one location (e.g., dots in the upper left of the screen). The trained motion type and location for each participant were selected prior to beginning the experiment, and were counterbalanced across the two motion types and four visual quadrants. Participants were required to take a short break after 20 minutes, and again after 40 minutes. Each training day, tracking speeds for each trial were calculated using two randomly interleaved staircases (see
Appendix A2 for details). At the conclusion of each training session, the mean of the two staircases’ final four reversals were used to calculate the initial trial speeds for the following training day.

After 6 days of training, post-training speed thresholds were determined using the same procedure as the pre-training assessment. The starting staircase speeds were the same for the post-training assessment (day 9) as they were for the pre-training assessment (day 2). In pilot experiments, we found that observers often showed a drop in performance on what they believed to be the last day of testing. Thus, participants completed an additional 1-hour session (day 10) after the post-training assessment, so that the critical post-training measure (day 9) would not occur on the final day of the experiment. Because our pilot data suggested that these “extra day” data should not be analyzed, we only tested participants for 1-hour on day 10, which was not enough time for all of the staircases to asymptote (i.e., not enough reversals could be completed in an hour to provide comparable speed-threshold estimates).

Control participants completed the same practice and assessment sessions as the training participants, but completed no training between the pre-training and post-training assessment; these control participants did not come into the lab or have any contact with the lab during the interval between the two assessments. Although no-contact control groups are a problem for cognitive training studies claiming generalization of training benefits (Boot, Simons, Stothart, & Stutts, 2013), such a strategy is actually advantageous when reporting specificity of training benefits, as it allows measurement of the amount of the post-training improvement attributable to taking the assessment a second time. The source of any improvement following an active-control task would be less clear, and could potentially be the result of enhanced attentional capacity induced by the control task, complicating claims about the specificity of training benefits.
Although we cannot rule out the possibility that the no-contact control participants displayed greater motivation than the training participants following their extended break (potentially producing performance gains beyond test-retest improvement), this possibility is very unlikely given that active controls typically perform more similarly to training subjects than no-contact controls (Melby-Lervåg & Hulme, 2013; Au et al. 2015).

Stimuli

Two different multiple-object tracking stimulus types were used during the experiment (Figure 1.1), both of which required tracking two target items moving amongst two distractor items for 6 seconds (510 frames at 85 Hz; 40 cm X 30 cm CRT monitor; 50 cm viewing distance, 122 cd/m² background luminance). One task required tracking two of four moving dots, while the other required tracking one spoke on each of two rotating pinwheels (each pinwheel had two spokes, one of which had to be tracked).

Each trial occurred in one quadrant of the screen. The black translating dots (diameter = 1.1°) were contained within a 14.8° x 14.8° invisible box, centered at 45° between the horizontal and vertical midline along an invisible circle of radius 13.4°. A minimum spacing of 2.2° was maintained between the dots. The black pinwheels (width = 5.1°) were contained within the same 14.8° x 14.8° invisible box, with each pinwheel centered 22.5° from the center of the box along the invisible circle of radius 13.4°. The pinwheels rotated and changed direction independently of one another, with changes in spin direction occurring a minimum of 75 frames apart and a maximum of 400 frames apart; each pinwheel had a 1/200 chance of changing spin direction at each frame between the minimum and maximum. At the start of each trial, two of the four items were designated as targets by blinking. The target items then gradually faded to the
color of the distractor items during the first second of motion. During the 6 seconds of motion, subjects were required to maintain central fixation by looking at a crosshair (width = .6°) at the center of the screen. If participants broke central fixation (>2° from center, monitored using EyeLink 1000, SR Research), the trial was terminated and not used for calculating the participant’s tracking-speed threshold. Blinking during the 6 seconds of motion did not count as a broken fixation. After 6 seconds, the targets stopped moving, and participants were required to try to identify the two target items by selecting them with a mouse click. Trials were only marked as correct when both target items were successfully identified.

Due to experimenter error, jpeg compression of the pinwheel stimuli caused the target items to appear slightly darker (7.2 cd/m²) than the distractor items (8.5 cd/m²) for the pinwheel stimuli for the dot training group. This error did not occur for the black (5.8 cd/m²) dot stimuli, and was not present for pinwheel training group or the control group. Although a potential concern, we are confident that this error did not influence the results of the dot training group (the only group exposed to the error) for several reasons. First, the difference was subtle, and was reported by only one observer who completed an experimental session with near perfect accuracy, despite the pinwheels spinning at impossibly fast speeds (> 1200 deg/s; this subject was removed from the experiment). No other observers appeared to notice this error, as none achieved such high performance in any experimental session. Second, if participants had noticed this error and performed well on the pre-training task, then it would artificially look like they improved less on the post-training tasks. However, the stimulus error did not appear to result in inflated performance in the pre-training assessment for the pinwheel stimuli: an independent-samples t-test revealed that the dot training group’s baseline performance for pinwheels with the error (M = 291.3 deg/s, SD = 85.3 deg/s) and the pinwheel training group’s baseline performance
for pinwheels without the error ($M = 292.4$ deg/s, $SD = 74.9$ deg/s) was equivalent ($t(30) = 0.04$, $p = .97$). Finally, although this error could have artificially produced increases in the pinwheel transfer conditions (new motion and both new) relative to the dot conditions (trained and new location) if the dot training group had picked up on the error in the post-training assessment, the dot training grouped displayed greater gains for the dot-tracking conditions than for the pinwheel-tracking conditions (meaning this outcome would have worked against our findings of specificity). In short, with the exception of one subject, participants did not appear to notice this stimulus error, and if they had it would work against the ultimate conclusions drawn based on data from both training groups combined.

Participants

Participants ($N = 48$, $M_{age} = 23.5$, 21 female, 27 male) were recruited from Harvard University and the Cambridge, MA community via posters describing the study. Participation was limited to individuals between the ages of 18-35 with normal or corrected to normal vision; those with corrected to normal vision were required to wear contacts during their participation. Participants received $10/hour compensation, plus an additional $25 completion bonus at the end of day 5 (for dot training and pinwheel training subjects) and day 10. To increase participant engagement, participants also received performance-based bonus pay of up to $5 per day.

Before beginning subject recruitment, a target sample of 16 participants for each of the three groups (dot training, pinwheel training, control) was decided upon for inclusion in our final analysis. This number was selected after examining effect sizes of interest from pilot data. Also before beginning recruitment, we decided to replace any subjects in the dot training and pinwheel training groups who failed to display at least 25% improvement in at least one of the
four experimental conditions (the criterion was applied to all conditions so that we would not bias the sample towards participants who showed spuriously high improvement in the training condition). Because the study’s goal was to examine whether training benefits would generalize, we wanted to include only participants who showed at least moderate training benefits. Control participants, however, were not replaced for failing to improve by 25% in at least one of the four tasks; although this may have slightly underestimated the amount of test-retest improvement in the control condition relative to the four training conditions, this was a conservative analysis strategy given our conclusions of training specificity. Two subjects (one dot training and one pinwheel training subject) were replaced for failing to improve by 25% in at least one experimental condition. An additional five subjects (two dot training, one pinwheel training, and two control subjects) were replaced for having an excessive amount of fixation breaks during their baseline or final assessment session (> 3 standard deviations from the mean broken fixations during assessment), indicating extreme difficulty keeping fixation. Finally, a one dot training subject was excluded after being found using a cell phone during trials of the final assessment. Seven additional subjects were replaced after dropping out of the experiment during the training period (three dot training, one pinwheel training, and three control participants). Had subject replacement not occurred, the only difference in significance testing would have been between the new location condition and the control condition, which would not have been significantly different without subject replacement (see Appendix A3). Although this lack of a difference between the new location and control conditions would have actually better supported our claims of training specificity, the exclusion criterion was determined before running the study, and we believe our data is more reliable following subject replacement.
Results

For each tracking task, the dependent measure was improvement in tracking speed from baseline, calculated as (post-training speed – pre-training speed)/pre-training speed. As shown in Figures 1.3 and 1.4, all conditions displayed significant improvement following training (see Appendix A4 for condition means and standard deviations). Considering first only the improvement of participants who completed training sessions (i.e., dot training and pinwheel training subjects), a mixed-factors ANOVA with within-subjects factor condition (trained, new motion, new location, both new) and between subjects-factor training task (dot training, pinwheel training) revealed a main effect of condition, \( F(3,90) = 21.82, p < .001 \). The main effect of training group (\( F(1,30) = 0.06, p = .80 \)) and the interaction of condition x training group (\( F(3,90) = 0.05, p = .98 \)) were not significant, indicative of the consistent pattern of improvement between the dot and pinwheel training groups (Figure 1.4; see Appendix A5 for individual subject distributions).

For both the dot training (dot) and pinwheel training (pw) groups, comparisons between conditions using paired-samples t-tests revealed that improvement for the trained condition was significantly greater than for the new motion condition \( (t_{dot}(15) = 3.26, p_{dot} = .005, d_{dot} = .97; t_{pw}(15) = 4.11, p_{pw} < .001, d_{pw} = 1.50) \), new location condition \( (t_{dot}(15) = 2.51, p_{dot} = .02, d_{dot} = .87; t_{pw}(15) = 4.18, p_{pw} < .001, d_{pw} = .88) \), and both new condition \( (t_{dot}(15) = 4.20, p_{dot} < .001, d_{dot} = 1.28; t_{pw}(15) = 5.29, p_{pw} < .001, d_{pw} = 1.78) \). Improvement for the new location condition was significantly greater than for the both new condition \( (t_{dot}(15) = 2.26, p_{dot} = .04, d_{dot} = .59; t_{pw}(15) = 2.76, p_{pw} = .01, d_{pw} = .84) \). Neither the improvement difference between the new location and new motion conditions \( (t_{dot}(15) = 1.18, p_{dot} = .26, d_{dot} = .27; t_{pw}(15) = 1.56, p_{pw} = .18) \)
.14, \( d_{pw} = .49 \) nor the new motion and both new conditions (\( t_{dot}(15) = 1.46, p_{dot} = .17, d_{dot} = .25; t_{pw}(15) = 1.86, p_{pw} = .08, d_{pw} = .46 \)) was statistically significant.

To explore whether improvement for the trained, new motion, new location, and both new conditions was greater than would be expected from test-retest related improvement, we compared improvement in each of these conditions to improvement for the no-contact control condition using independent-samples t-tests. For each control participant, four improvement scores were obtained (one for each motion type/location combination). An overall improvement score for each control subject was calculated using the mean improvement in tracking speed across the four motion type/location combinations. Results were again consistent between the dot training and pinwheel training groups. Of primary interest, independent-sample t-tests revealed that the trained condition showed significantly greater improvement than the control condition (\( t_{dot}(30) = 4.28, p_{dot} < .001, d_{dot} = 1.46; t_{pw}(30) = 4.92, p_{pw} < .001, d_{pw} = 1.68 \)), but that the both new condition did not (\( t_{dot}(30) = 0.15, p_{dot} = .88, d_{dot} = .05; t_{pw}(30) = 0.13, p_{pw} = .90, d_{pw} = -.04 \)).

Of secondary interest, improvement for the new location condition was greater than that for the control condition (\( t_{dot}(30) = 2.23, p_{dot} = .03, d_{dot} = .76; t_{pw}(30) = 2.26, p_{pw} = .03, d_{pw} = .77 \)), but improvement for the new motion condition was not (\( t_{dot}(30) = 0.95, p_{dot} = .35, d_{dot} = .32; t_{pw}(30) = 1.16, p_{pw} = .26, d_{pw} = .40 \)). See Appendix A6 for model comparisons using mixed effect analyses, which compare all conditions in a single analysis, and support the same conclusions.

We next tested for baseline differences in standardized threshold speed during the pre-training assessment, in an effort to rule out baseline differences as the cause of the differential training improvement found between conditions. Again considering first only the improvement of participants who completed training sessions (i.e., dot training and pinwheel training subjects), a mixed-factors ANOVA with within-subjects factor condition (trained, new motion, new
location, both new) and between subjects-factor training task (dot training, pinwheel training) revealed no main effects of condition ($F(3,90) = 0.48, p = .70$) or training task ($F(1,30) = .15, p = .70$), nor a condition x training task interaction ($F(3,90) = 1.43, p = .24$), indicating no reliable differences between training conditions at baseline (Day 2 in Figure 1.3). We next used independent-samples t-tests to test for differences in pre-training speed thresholds between control condition and the other four conditions (aggregated across the dot and pinwheel training groups). These analyses revealed no significant baseline difference between the control condition and the trained ($p = .38$), new motion ($p = .72$), new location ($p = .44$), or both new conditions ($p = .68$).

![Figure 1.3: Speed Thresholds and Learning Curve. The trained, new motion, new location, and both new conditions are aggregated across the dot and pinwheel training groups (see Appendix A7 for individual group learning curves). A different staircase procedure was used for the training days (days 3-8) than was used during the two assessment days (days 2 and 9). Error bars represent SEM.](image-url)
Figure 1.4: Training Results. Dot Training and Pinwheel Training subjects (N = 16 each) trained on their respective training task in one quadrant (shown as dots in the top-left quadrant for illustration here, but counterbalanced between subjects in the actual experiment), while control subject (N = 16) completed no training. Speed thresholds were measured before and after training, and the y-axis shows the percent increase in speed thresholds after training. All tasks were expected to show some improvement due to practice effects. However, the improvement on the trained task in the trained location (Trained) was greater than the improvement when the motion type was different (New Motion), the location was different (New Location), or both were different (Both New) than the training task. Improvement for the trained condition was also greater than for the control condition. The New Location condition showed greater improvement than the Both New condition and the control condition, but no other differences were reliable. Improvement for each condition was significantly greater than 0. Error bars represent SEM.

Discussion

The specificity of training benefits found in this study indicates that training did not increase any general attentional capacity, but instead enhanced attention’s ability to perform operations over representations specific to the training task, supporting the expertise-building
hypothesis of attentional training. Training benefits for a trained motion type in a trained retinotopic location (trained condition) displayed incomplete generalization to tasks differing in seemingly superficial features, such as motion type (new motion), retinotopic location (new location), or both of these characteristics (both new). Furthermore, improvement for the both new condition was no greater than for a control group that performed no training, indicating that no generalization occurred when the properties of motion type and retinotopic location were not shared. Although improvement for the new location condition was significantly less than for the trained condition, improvement for new location was greater than for the both new and control conditions, suggesting that partially shared features between trained and untrained tasks may allow limited generalization. If the large improvement for the trained condition had been the result of enhanced attentional capacity, however, performance gains should have generalized to all the similar untrained tracking conditions.

Since the improvement in the trained condition was not the result of enhanced attentional capacity, at least two alternative possibilities exist. One possibility is that only representations specific to the training task were altered during training (Figure 1.1), resulting in more precise encoding of target locations. This explanation is compatible with the specificity typically found in perceptual learning studies (Karni & Sagi, 1991; Poggio et al., 1992), where the training task is limited by the quality of representational encoding. If indeed only task-specific representations are enhanced during training, training benefits should generalize to untrained tasks requiring these same representations, even if the untrained tasks require a different attentional capacity. For example, improved tracking of translational motion in the upper-left visual field would be expected to generalize to a search task using the same stimuli, a possibility that could be tested in future studies. However, because the attentional tracking paradigm used here appears to be
limited primarily by attentional processing rather than representational quality (Alvarez & Franconeri, 2007; Culham et al., 1998), we favor a second possibility: training enhanced the coordination between an attentional capacity and representations specific to the training context. That is, rather than improving the quality of perceptual representations specific to the training task, training instead enabled a general attentional capacity to access those representations more effectively. This explanation is compatible with theories positing that enhanced access to representational content is critical for training-induced performance gains (e.g., Ahissar & Hochstein, 2004), and predicts that training benefits will generalize only to tasks requiring attentional expertise that has been enhanced during training (i.e., the connection between the general attentional capacity shared by the tasks and the representations specific to the training task must be enhanced, see red arrow in Figure 1.1). Therefore, neither a shared attentional capacity nor shared representations between a training and transfer task alone would be sufficient for producing generalization.

Although other studies have reported specificity of training benefits between tasks limited by cognitive control mechanisms, (Gaspar, Neider, Simons, McCarley, & Kramer, 2013; Melby-Lervåg & Hulme, 2013; Thompson et al., 2013), to our knowledge we are the first to demonstrate such minimal generalization of large training benefits between nearly identical attention-limited tasks (all tasks required tracking two moving targets) that were shown to require a common attentional capacity (see Appendix A1). Because of this specificity, we claim that training enhances content-specific attentional coordination rather than general attentional capacities, a conclusion that assumes the attentional tracking tasks in this study use and are limited by the same attentional mechanisms. This assumption can be supported in several ways. First, we ran a preliminary study using the attentional operating characteristic method (see
Appendix A1), demonstrating a performance tradeoff between the tasks that is evidence of a common attentional capacity. In previous studies failing to find generalization following training, it is often unclear whether the training and transfer tasks rely on the same capacity (particularly in studies training working memory, which appears to have separate capacities for visual vs. verbal information (Baddeley & Hitch, 1974), visual vs. spatial information (Wood, 2011), and view-dependent vs. view-invariant information (Wood, 2009)). Second, previous research has suggested that objects tracked within a single visual hemifield (left or right) are maintained by a common attentional resource (Alvarez & Cavanagh, 2005); in the present study, the trained and untrained tasks always occurred within the same visual hemifield. Third, neuroimaging research has implicated the intraparietal sulcus as a critical region across a variety of attentional tracking tasks, including translational (Culham et al., 1998) and rotational motion (Shim, Alvarez, Vickery, & Jiang, 2009); baseline performance for the two types of motion was also highly correlated in our subjects (Appendix A8). Finally, although using target speed as the study’s dependent measure (rather than the number of items tracked) may intuitively seem to introduce low-level representational challenges to the tracking task (in addition to attentional limitations), previous research has indicated that observers have sufficient representational precision for tracking items at high speeds, yet are unable to access these representations efficiently when attention is divided (Alvarez & Franconeri, 2007). Furthermore, both the speed at which objects can be tracked and the number of objects that can be tracked appear to be limited by a common capacity (Thompson, Gabrieli, & Alvarez, 2010). Therefore, we are confident that tracking performance was primarily attention-limited in this study despite target speed being the dependent measure, and predict a similar pattern of results would occur if the number of targets were increased during training instead of target speed.
Implications for Cognitive Training

Inconsistency has plagued training paradigms attempting to enhance the capacity of cognitive control processes critical to everyday functioning, such as attention (Green & Bavelier, 2003) and working memory (Jaeggi et al., 2008). Although we cannot speak directly to the mechanisms underlying generalization in these studies (which often are completed over a longer training period with a more diverse range of training tasks), our results do provide direct evidence against the logic motivating such training paradigms: i.e., that generalization of training benefits is expected between tasks that rely on a common cognitive capacity. Our results indicate that training can produce content-specific attentional expertise, rather than enhancing general attentional capacities; therefore, simply selecting training tasks that share general control mechanisms with outcome measures of interest is insufficient for producing generalization. Until the parameters necessary for producing generalized training benefits are established, consumers interested in cognitive enhancement should be aware that improvement on training tasks is not necessarily evidence of any improvement to general cognitive functioning.

Although the specificity found in the present study challenges the capacity-enhancing hypothesis assumed by many cognitive training studies, we believe that generalization of training benefits is possible under the expertise-building framework we have proposed, particularly if training produces enhanced attentional coordination necessary for the completion of untrained outcome measures. We speculate such generalization may occur when training enhances coordination between distinct control mechanisms (a type of coordination potentially critical to multitasking; Anguera et al., 2013), or when training improves multiple forms of attentional expertise that when combined produce improvement in untrained tasks (e.g., Xiao et al., 2008). Importantly, even training programs that fail to enhance attentional processing may still be
beneficial, particularly if learned strategies (e.g., mnemonic training; Verhaeghen, Marcoen, & Goossens, 1992) or placebo effects produce improvement in desirable outcome measures.

**Conclusions**

In summary, our results suggest that training benefits for attentional tracking are dependent on enhanced coordination of attention with content-specific representations, rather than resulting from an enhanced attentional capacity. We believe the general inconsistency of cognitive training programs is due in part to a misconception that the capacity of cognitive control mechanisms can easily be enhanced in one context for use in another, ignoring the critical importance of content-specific representations in obtaining training benefits. We hope our results will motivate investigation into whether and how enhancing attentional expertise can produce generalized training benefits, potentially leading to more effective and reliable cognitive training paradigms.

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Chapter 2

Hemifield-specific control of spatial attention and working memory:

Evidence from hemifield crossover costs

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Abstract

Attentional tracking and working memory tasks are often performed better when targets are divided evenly between the right and left visual hemifields, rather than contained within a single hemifield (Alvarez & Cavanagh, 2005; Delvenne, 2005). However, it remains unclear whether this bilateral field advantage reflects hemifield-specific control of attention and working memory, or instead results solely from hemifield-limited spatial interference during encoding. 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 to 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.
Hemifield-specific control of spatial attention and working memory:
Evidence from hemifield crossover costs

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 to 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 subjects 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 appeared 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; Delvenne, 2005; Delvenne, Castronovo, Demeyere, & Humphreys, 2011; 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.
The *exclusively spatial interference* account of the bilateral field advantage posits that there is stronger interference between attended targets that appear within the same hemifield than in separate hemifields, possibly because attention suppresses cortically neighboring representations (Franconeri, Alvarez, & Cavanagh, 2013; Störmer, Alvarez, & Cavanagh, 2014). 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 primary visual cortex, while 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, Jonathan, & Scimica, 2010; Liu et al., 2009; Störmer, et al., 2014). The *exclusively spatial interference* account of the bilateral field advantage posits this hemifield-limited spatial interference is the sole cause of the bilateral field advantage (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; Delvenne, 2005; Holcombe & Chen, 2012; Umemoto et al., 2010), contributing to the bilateral
field advantage as well. On this account, bilaterally presented items may be processed by two separate high-level control systems (one control system for each hemifield), while 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. Differentiating between these two accounts 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. If high-level control is also specific to each hemifield in healthy individuals, then maintaining target information should become more difficult when bilaterally presented targets simultaneously cross between the two hemifields, as hemifield-specific control systems would be required to exchange their information with one another. Alternatively, if high-level control is not specific to each hemifield and the bilateral field advantage occurs solely from spatial interference between representations, then maintaining target information should not
become more difficult as targets move between the hemifields (provided spatial interference between targets is controlled for). Therefore, difficulty maintaining target items that cross between the hemifields would provide evidence that hemifield-specific processing continues beyond early sensory regions, and into high-level control of attention and memory.

To test whether maintaining targets becomes more difficult when they move between the hemifields, observers in the present study performed either an attentional tracking or working memory task. In both types of tasks, target items were initially presented in diagonally opposite quadrants (e.g., top-left and bottom-right). After a delay, the targets shifted on the screen, 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 due to items moving within versus between the hemifields. Therefore, if only early stages of visual processing are hemifield-specific, observers should perform equally well when items move within versus 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 and 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 to unilaterally (Alvarez & Cavanagh,
2005), a result that has been interpreted as independent control of attentional tracking in each hemifield. However, this extreme bilateral field advantage can also be accounted for by a single attentional control process that has great difficulty tracking cortically nearby targets within a single hemifield, but little difficulty tracking cortically distant targets divided between the hemifields (Franconeri et al., 2010; Störmer et al., 2014). To test whether hemifield-specific attentional 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 not be sufficient for concluding the existence of hemifield-specific tracking mechanisms (due to the possibility of differential spatial interference between targets during between- versus within-hemifield movements, which we examine in Experiment 1B), a between-hemifield crossover cost is a necessary result for making such a conclusion.

**Method**

**Participants**

Sixteen 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 and G*Power 3.1 (Faul, Erdfelder, Lang, & Buchner, 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/m²) dots presented in each quadrant of a gray (19.5 cd/m²) square background (1200 x 1200 pixels), which was centered on the screen (1920 x 1200 pixels, refresh rate = 60 Hz, viewing distance = 56 cm). The midpoints of each of the four dot pairs were located 90 degrees 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/m²) fixation cross of diameter .8° was presented at the center of the screen.

**Figure 2.1**: Design of Experiment A. Target dots in diagonally opposite quadrants were cued before fading to black. Dot pairs rotated locally for 3000 ms before undergoing a global shift. During the global shift, all dot pairs shifted 45° along an imaginary circle (depicted with dashed line above) either clockwise or counterclockwise, before either continuing for another 45° in the same direction to a new location (Exp. 1A and Exp. 1B cross trials), or shifting 45° in the opposite direction back to their original locations (Exp. 1B return trials). After reaching their final locations, dot pairs rotated in place for another 3000 ms before one of the pairs containing a target was cued for response. A clockwise shift to a new location (between-hemifield) is depicted here.

**Procedure**

See Figure 2.1 for a depiction of experimental design. At the beginning of each trial, a pair of black dots was presented in each quadrant of the 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. After rotating in place for 3000 ms, all four dot pairs shifted 90 degrees 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 (for example, dot pairs moving horizontally between hemifields were always oriented vertically as they crossed the vertical midline; see Figure 2.1); this prevented two targets from being within the same hemifield during between-hemifield movements (besides one frame where the target dots were directly on the midline between hemifields). 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 condition), 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 3000 ms before coming to a stop. Once the dots came to a stop, one of the two pairs containing a tracked target was cued 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 cued pair was the tracked target using a mouse click. Observers were given feedback following 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 required to keep central fixation during all trials, which was monitored via an eye-tracking device (EyeLink 1000, SR Research, Ottawa, ON, Canada) – if observers broke fixation during tracking
(>2° from fixation), the trial was terminated and restarted. Participants completed 4 blocks of 24 trials each.

Prior to 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; \( M = 371.7 \text{ deg/s}, SD = 142.8 \text{ deg/s} \)) was used during the main experimental trials.

Results

Observers were better at identifying target dots following within-hemifield movements \((M = 77.2\%, SD = 12.1\%)\) than following between-hemifield movements \((M = 66.7\%, SD = 13.4\%\); \( t(15) = 3.95, p = .001, d_z = .99; \) see Figure 2.2A). This result is consistent with hemifield-specific control processes for attentional tracking, which must exchange information during between-hemifield movements.

Experiment 1B: Control For Potential Midline Effects

To rule out the possibility that time at the vertical midline explains the between-hemifield crossover cost, we replicated the conditions from Experiment 1A, and added two new return conditions (Figure 2.2B), 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 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 participants should perform worse for horizontal shifts than for vertical shifts only for the cross conditions, and not for the return conditions (where the targets remain within their original hemifields).

Method

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 and G*Power (Faul et al., 2007), 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 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, 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). Participants completed 8 alternating blocks of cross and return trials, with each block containing 24 trials.

**Results**

A 2 (movement direction: horizontal vs. vertical) x 2 (trial type: cross vs. return) repeated-measures ANOVA revealed a significant movement direction x trial type interaction ($F(1, 39) = 14.67, p < .001, d_z = .61$). Replicating Experiment 1A, when items moved to a new location, observers were better at identifying target dots after vertical shifts within-hemifield ($M = 78.8\%, SD = 11.1\%$) than after horizontal shifts between-hemifield ($M = 69.2\%, SD = 10.2\%$; $t(39) = 6.28, p < .001, d_z = .99$; see Figure 2.2B). When items returned to their original locations, however, there was no significant difference in tracking performance for horizontal ($M = 78.4\%, SD = 10.4\%$) versus vertical shifts ($M = 77.4\%, SD = 10.3\%$; $t(39) = 0.66, p = .52, d_z = .10$).
Figure 2.2: 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 Exp. 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 non-target quadrants (see Figure 2.1), but are not depicted here for clarity.

Discussion: Experiments 1A & 1B

Experiment 1A revealed a cost for attentively tracking targets that move between the hemifields, while Experiment 1B demonstrated that this cost was not due to difficulty tracking at the border between hemifields. These results provide evidence for hemifield-specific control of attentional tracking, as a single attentional control process cannot account for a crossover cost that occurs despite equivalent tracking ability 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.

**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, on the other hand, require initial 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 appear to 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) following 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 appears 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 interference 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), 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).

**Method**

**Participants**
Sixty observers (30 female, $M_{age} = 34.7$) were recruited via Amazon Mechanical Turk and participated after giving informed consent. This sample size was selected using the results of pilot data and G*Power (Faul et al., 2007), which indicated that 60 observers would result in greater than 95% power to an effect of $d_e = 0.50$.

**Stimuli**

At the beginning of the experiment, a white square with a red border (650 x 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 2x2 grids (150 x 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 cue 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 2x2 grids appeared at diagonally opposite corners (e.g., top-left and bottom-right) of the screen. After a 500 ms delay, black dots appeared in two of the four cells of each grid. Both grids never contained the same arrangement 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 cells (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
Figure 2.3: Design of working memory location trials (Experiment 2A – 3B), color trials (Experiment 3A), and identity trials (Experiment 3B). After targets where 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 trial 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).

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, following which a cell in one grid was cued by being filled with a dot for 500 ms. Participants used a keypress to indicate whether the cued cell had previously contained a dot (pressing “s” if it had, or “d” if it had not). Participants completed 64 trials, receiving accuracy feedback following 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 place instead of moving to new locations.
Results

Observers were more accurate reporting whether the cued cell had previously contained a dot following within-hemifield movements ($M = 86.8\%$) than following between-hemifield movements ($M = 79.7\%$; $t(59) = 5.74, p < .001, d_z = .74$; see Figure 2.4A). 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 versus within their original hemifield (see Appendix B).

![Figure 2.4](image-url)

**Figure 2.4**: 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 Exp. 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). Although the remembered dots were not present as the empty grids moved to the midline during Experiment 2A, a reduced 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 2.4B), 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.

Method

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 and G*Power (Faul et al., 2007), which indicated that 100 observers would result in greater than 95% power to detect an interaction effect size of \(d_x = 0.40\).
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 trials) and one block of return trials (64 trials), the order of which was counterbalanced between participants.

Results

A 2 (movement direction: horizontal vs. vertical) x 2 (trial type: cross vs. return) repeated-measures ANOVA revealed a significant movement direction x trial type interaction ($F(1, 99) = 22.60, p < .001, dz = .48$; see Figure 2.4B). 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 ($M = 79.1\%, SD = 14.1\%; t(99) = 6.66, p < .001, dz = .67$). When items returned to their original locations, however, there was no significant difference in tracking performance for vertical ($M = 89.3\%, SD = 13.0\%$) versus horizontal shifts ($M = 88.7\%, SD = 14.1\%; t(99) = 1.00, p = .32, dz = .10$).
Discussion: Experiments 2A & 2B

The between-hemifield crossover cost for the working memory task in Experiments 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 crossover 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, as 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 inference.

Previous research has documented behavioral (Oksama & Hyönnä, 2004; Lapierre et al., 2017) 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 & 1B) and spatial working memory (Experiments 2A and 2B) suggests that one of these shared mechanisms is hemifield-specific control over 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 from spatial information being maintained by lateralized control systems, whereas identity features (such as color) are maintained by non-lateralized, global control systems. This possibility is consistent with non-spatial 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 (Sàenz, Buraças, & Boynton, 2003; Störmer & Alvarez, 2014). In the present study, we test whether a dissociation occurs for maintaining spatial information (relative location) versus identity information (color) in working memory as items move between the hemifields. If the previously observed differences in spatial versus feature-based attention and working memory are a result of lateralized control being specific to spatial information, then a crossover cost is expected for spatial working memory, but not color working memory.

**Method**

**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 simulated data (which assumed no difference between within- and between-hemifield performance for the color working memory task) and G*Power (Faul et al., 2007), 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 x 155 pixels) instead of grids, which were each filled with a different color 180 degrees 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 (see Figure 2.3) 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 filled with color (either the circle’s original color, or a different color 45 degrees 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 cued 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) was varied between the location and color conditions. Participants were instructed to avoid rehearsing color names, as well as to repeat the word “the” in their heads during completion of the experiment. 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 Experiment 2A and 2B discussion). Observers completed one block of spatial working memory trials (64 trials) and one block of color working memory trials (64 trials), 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) x 2 (memory type: location vs. color) repeated-measures ANOVA revealed a significant hemifield movement x memory type interaction ($F(1, 99) = 31.43, p < .001, d_z = .56$; see Figure 2.4C). Again replicating Experiment 2A, for the spatial working memory task of remembering dot locations, observers were better at identifying target dots following vertical shifts within-hemifield ($M = 86.7\%, SD = 13.5\%$) than following horizontal shifts between-hemifield ($M = 81.4\%, SD = 13.2\%; t(99) = 6.26, p < .001, d_z = .63$). 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 ($M = 83.8\%, SD = 10.5\%$) versus horizontal shifts between hemifield ($M = 85.5\%, SD = 10.1\%; t(99) = 1.88, p = .06, d_z = -.19$).

![Figure 2.5](image)

Figure 2.5: Results of Experiments 3A and 3B. Error bars represent within-subject SEM (Cousineau, 2005). A: Observers displayed a between-hemifield cost for remembering dot locations (location conditions, replicating Experiment 2A), but no performance difference was found for color working memory trials when items moved within versus between the hemifields. B: In addition to again replicating Experiment 2A (location conditions), no between-hemifield cost was found for remembering the identity of abstract fractals.
Experiment 3B: Spatial vs. Identity Working Memory

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

Method

Participants

One hundred fifty observers ($M_{age} = 37.3$, 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 and G*Power (Faul et al., 2007), 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 x 200 pixels) - all other aspects of the display were the same as the spatial working memory task described in Experiment 2A (see Figure 2.3). 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.
(see Figure 2.3) requiring them to remember the identity of a fractal image presented in each hemifield. After the fractals were briefly presented inside a 200 by 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 hemifields or horizontally between hemifields. After the square borders reached their final locations, a fractal image appeared within one of the square borders (either the original fractal image, or a new fractal image). Observers used a keyboard press to indicate whether this fractal was the same or different from the fractal that had previously occupied the square border (pressing “s” if it was the same fractal, or “d” if it was a different fractal). New fractal images were always different from both of the fractals presented during the encoding period. 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) was varied between the location and fractal identify conditions. Participants were instructed to avoid using rehearsal strategies while completing the task, as well as to repeat the word “the” in their heads during completion of the experiment. Observers completed one block of spatial working memory trials (64 trials) and one block of fractal identity working memory trials (64 trials), 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.
Results

A 2 (hemifield movement: within vs. between) x 2 (memory type: location vs. identity) repeated-measures ANOVA revealed a significant hemifield movement x memory type interaction ($F(1, 149) = 14.55, p < .001, d_z = .31$; see Figure 2.4B). Again replicating Experiment 2A, for the spatial working memory task of remembering dot locations, observers were better at identifying target dots following within-hemifield shifts ($M = 85.1\%, SD = 16.6\%$) than following between-hemifield shifts ($M = 80.1\%, SD = 14.7\%$; $t(149) = 6.70, p < .001, d_z = .55$). 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 ($M = 77.4\%, SD = 14.4\%$) versus between-hemifield shifts ($M = 76.5\%, SD = 13.1\%$; $t(149) = 0.95, p = .34, d_z = .08$).

Discussion: Experiments 3A & 3B

Observers displayed a between-hemifield crossover cost for a spatial working memory task, but not for color (Experiment 3A) or fractal identity (Experiment 3B) 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 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 appears that what 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), as 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.

**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 in early sensory areas (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 after controlling for possible interference between items at the vertical midline between hemifields, 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 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 & 2B). Because a drop in performance 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 (Experiment 3A) or identity (Experiment 3B) 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 versus identity information in working memory (Courtney, Ungerleider, Keil, & Haxby, 1996; Mecklinger & Muller, 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 (Sàenz, et al., 2003; Störmer & Alvarez, 2014) lead us to predict that a between-hemifield crossover cost would not occur for identity feature-tracking tasks, a prediction that can be tested in future experiments.

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, as 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 the hemifield-specific control systems would be imperfect, producing the between-hemifield crossover cost. 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, Mance, Horowitz, Wolfe, & Vogel, 2014). Simultaneous representation of both the target departing the hemifield and the target arriving from the other hemifield could allow hemifield-specific buffers to exchange their information, but this transfer would be imperfect due to interference resulting from both targets being temporarily represented within each buffer. Importantly, by this account spatial interference during between-hemifield movements is not an alternative to hemifield-specific control, but instead the result of it – with a single control system governing the entire visual field, information could be transferred between the hemifields without needing the soft handoff that leads to spatial interference. Therefore, spatial interference may play a critical role in the between-hemifield crossover cost, as a consequence of hemifield-specific control systems needing a way to avoid complete information loss during between-hemifield movements.

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). As both the “soft-handoff” and “contralateral-bias” accounts of hemifield-specific control are consistent with the between-hemifield crossover cost, future work is needed to clarify the precise mechanisms of information transfer between hemifields.

**Relationship to Patient Findings**

The behavior of hemispatial neglect (Posner, Walker, Friedrich, & Rafal, 1984) and split-brain (Luck et al., 1989, 1994) patients 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, as healthy observers displayed a between-hemifield crossover cost incompatible with a single attentional spotlight. 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, as the consequences of hemifield-specific control likely vary greatly with changes to neural structure. For example, hemispatial neglect appears to result from an inter-hemispheric imbalance arising from damage to one hemisphere (Corbetta & Shulman, 2011), while crossover costs occur despite both hemispheres functioning normally. 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 bilateral hemispheric processing may minimize the impact of brain damage, as having both hemispheres capable of performing the same computation could allow relatively normal functioning as long as one hemisphere remained intact (Schapiro et al., 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 versus identity information, which are processed separately (to some degree) in the dorsal and ventral streams of the visual system, respectively (Goodale, Milner, Jakobson, & Carey, 1991; Milner & Goodale, 1992; 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. Non-spatial 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 appears 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 exploring 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, as it is easier to perceive two pairs of ambiguously moving dots 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. 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.

Conclusion

In summary, 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 indicate 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 investigation into the mechanisms of information transfer between the hemifields.
Chapter 3

Hemifield-specific information is exchanged as targets move between the hemifields

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Abstract

Tracking moving targets with attention is more difficult when targets cross between the left and right visual hemifields (compared to when targets move within their original hemifields), providing evidence for separate control of attentional tracking in each hemifield (Strong & Alvarez, in prep). There are at least two possible explanations for why separate control of tracking in each hemifield would lead to this between-hemifield cost. One possibility is that hemifield-limited attentional spotlights inefficiently exchange target information as targets cross between hemifields. A second possibility is that hemifield-specialized attentional spotlights continue to track their original targets after the targets cross between hemifields, but do so less effectively. To differentiate between these two possibilities, observers tracked two targets (one in each hemifield) that varied in both A) the number of times they crossed between hemifields and B) the time they spent within a new hemifield (Experiment 1). Tracking accuracy decreased as the number between-hemifield crosses increased, but was not influenced by the time targets spent in a new hemifield, consistent with an inefficient information exchange between hemifield-limited attentional spotlights. Experiment 2 showed that although observers have difficulty tracking targets that move between the hemifields using divided attention, the same between-hemifield cost does not occur when observers track a single target using focal attention. Together, these experiments show that hemifield-specific attentional spotlights exchange information as attended items move between the hemifields, and that the efficiency of this exchange depends on how attention is allocated throughout the visual field.
Hemifield-specific information is exchanged as targets move between the hemifields

Split-brain patients have demonstrated that the two cerebral hemispheres can function independently, with each hemisphere controlling visual processing in the contralateral visual hemifield when not connected by the corpus callosum (Kimura, 1973). Although initially only split-brain patients were thought to have separate “spotlights” of attention for each hemifield (Luck, Hillyard, Mangun, & Gazzaniga, 1989, 1994), more recently hemifield-specific attentional control has been demonstrated in healthy individuals as well. For example, healthy observers are better at dividing attention between the two hemifields than within a single hemifield, as though each hemifield has its own spotlight of attention (Awh & Pasher, 2000; Alvarez & Cavanagh, 2005). Additionally, observers have difficulty using attention to track multiple targets crossing between the hemifields (Strong & Alvarez, in prep), a finding again consistent with hemifield-specific attentional control (and incompatible with a single attentional spotlight). Although these findings provide evidence for hemifield-specific attentional spotlights, they do not explain how these spotlights represent information that moves between the left and right hemifields, a requirement of everyday tasks such as driving.

The present study uses the multiple-object tracking paradigm (Cavanagh & Alvarez, 2005; Pylyshyn & Storm, 1988) to explore how hemifield-specific attentional spotlights represent information moving between the hemifields. The first experiment provides evidence that these separate spotlights are limited to each hemifield, requiring an exchange of information in order to represent targets that move between the hemifields. The second experiment demonstrates that although this exchange results in information loss when attention is divided between the hemifields, hemifield-specific attentional spotlights are able to coordinate efficiently
when attention is deployed to only one hemifield. Together, these experiments reveal that attentional control is limited by the ability of hemifield-specific attentional spotlights to exchange their information with one another, and that the success of this exchange depends on whether attention is deployed to one or both hemifields.

**Experiment 1: Information Exchange Between Hemifield-Limited Spotlights**

There are at least two possible ways that separate attentional spotlights for each hemifield could represent information that moves between the hemifields (see Figure 3.1). The first possibility is an exchange of information between *hemifield-limited* attentional spotlights. This explanation posits that as attended information crosses between the hemifields, each hemifield-limited spotlight stops tracking its original departing information and begins tracking newly arriving information. This possibility is consistent with electrophysiological evidence that representation of an attentively tracked target shifts from one cerebral hemisphere to the other as the target moves between hemifields (Drew, Mance, Horowitz, Wolfe, & Vogel, 2014). Evidence for information transfer between hemifield-limited spotlights has also been demonstrated by a patient without a splenium (the posterior portion of the corpus callosum); this patient experienced difficulty tracking a single target that moved between hemifields (although still performing above chance levels), consistent with low-quality target information being transmitted between hemifield-limited attentional spotlights (Noudoost, Afraz, Vaziri-Pashkam, & Esteky, 2006). To account for the finding that healthy observers have difficulty tracking multiple targets that move between the hemifields (Strong & Alvarez, in prep.), an information exchange between hemifield-limited attentional spotlights would need to result in information loss when multiple targets are tracked simultaneously.
In contrast to an information exchange between hemifield-limited attentional spotlights, a second possibility is that hemifield-specialized attentional spotlights continue to track their original targets even after the targets move into a new hemifield. By this account, although separate attentional spotlights may be specialized for control of a particular hemifield, they have the ability to control attention in both hemifields. Consistent with this possibility, previous research has demonstrated that each cerebral hemisphere may have the capability to control tracking in the ipsilateral hemifield, despite typically controlling attention in the contralateral hemifield (Battelli et al., 2001; Battelli, Alvarez, Carlson, & Pascual-Leone, 2009). By maintaining their original information as targets move between hemifields, hemifield-specialized attentional spotlights could avoid a potentially inefficient information exchange. To account for the difficulty healthy observers have using divided attention to track targets that move between the hemifields (Strong & Alvarez, in prep.), each hemifield-specialized spotlight would need to have a graded tracking ability that is maximal in its specialized hemifield, and weaker in its non-specialized hemifield (see Figure 3.1).

Both the hemifield-limited and hemifield-specialized accounts of attentional spotlights offer plausible explanations for how information is represented while crossing between hemifields, while additionally accounting for difficulty maintaining information that moves between the hemifields using divided attention (Strong & Alvarez, in prep). However, each of these accounts makes fundamentally different claims about how information moving between the two hemifields is represented. The hemifield-limited spotlight account posits that an exchange of information is necessary in order to maintain information moving between the hemifields, while the hemifield-specialized account posits that no information exchange is needed. Additionally, these two accounts make very different claims about why observers have difficulty tracking
Figure 3.1: Two accounts of information transfer between hemifields. The hemifield-limited account posits that each attentional spotlight is limited to tracking in one hemifield, requiring the spotlights to exchange their information when items cross between hemifields. The hemifield-specialized account posits that although specialized for tracking in one hemifield, each attentional spotlight has the ability to control attention in both hemifields, avoiding the need for an information exchange when items cross between hemifields.

information that moves between the hemifields; the hemifield-limited account posits that this difficulty arises from an inefficient information exchange between attentional spotlights, while the hemifield-specialized account posits that this difficulty is a consequence of a graded tracking ability for each attentional spotlight. To differentiate between the hemifield-limited and hemifield-specialized accounts, observers in the present study tracked moving targets that varied in both A) the number of times they crossed between hemifields and B) the amount of time they spent in a new hemifield (versus their original hemifield). The hemifield-limited spotlights account predicts that tracking performance should decrease with increasing numbers of between-hemifield crosses, as hemifield-limited spotlights would have to inefficiently exchange information each time a between-hemifield cross occurred. In contrast, the hemifield-specialized
spotlights account predicts that performance should decrease as targets spend more time in a new hemifield, as each hemifield-specialized spotlight would be required to spend more time tracking in a hemifield that it was not specialized for. Therefore, tracking accuracy varying as a function of between-hemifield crosses would provide evidence for hemifield-limited attentional spotlights, whereas tracking accuracy varying as a function of time targets spend in a new hemifield would provide evidence for hemifield-specialized attentional spotlights.

Method

Participants

By bootstrap resampling a set of pilot data (N = 41; for an overview of using simulation techniques to estimate power, see Lane & Hennes, 2018), we determined that collecting data from 270 observers scoring above 60% across all conditions would result in 95% power to detect the pattern of effects observed in the pilot data (the five significant comparisons reported in Experiment 1 results). A total of 362 observers (204 male, M_{age} = 36.4) completed the experiment before 270 (M_{age} = 36.4, 150 male) scored above the 60% cutoff point; only this subset was used in the final analysis. All observers were recruited via Amazon Mechanical Turk and participated after giving informed consent.

Stimuli

At the beginning of the experiment, a white square with a red border (650 x 650 pixels) was presented in front of a black background 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 consisted of black dots presented in each quadrant of the white square background. The midpoints of each of the four dot pairs were located 90 degrees apart along an imaginary circle.
of radius 247.5 pixels with an origin at the center of the white square; in each quadrant, the midpoint of the dot pair was an equal distance from the horizontal and vertical midlines (150 pixels). Each dot had a diameter of 32 pixels, and the distance between the centers of each dot within a pair was 118 pixels. A black fixation cross of diameter 20 pixels was presented at the center of the white square.

**Figure 3.2:** Design of Experiment 1. Target dots in diagonally opposite quadrants were cued before fading to black. Dot pairs rotated locally for 2000 ms before undergoing a global shift. During the global shift, all dot pairs shifted 90° along an imaginary circle (either clockwise or counterclockwise) to new locations on the screen. Dot pairs then rotated locally for again for 2000 ms before undergoing another global shift. After reaching their final locations (after the second global shift), dot pairs rotated in place for another 2000 ms before one of the pairs containing a target was cued for response. Two clockwise shifts are depicted in this example, resulting in target dots first moving between-hemifield and then within-hemifield.
**Procedure**

See Figure 3.2 for a depiction of experimental design. Observers were instructed to keep central fixation during all trials. At the beginning of each trial, a pair of black dots was presented in each quadrant of a white 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 white with a black border (3 cycles, 1 Hz). The target dots gradually faded from white to black (for 1000 ms) as the dot pairs begin rotating within each quadrant, randomly changing spin direction. After rotating in place for 2000 ms, all four dot pairs underwent a global shift, moving 90 degrees along an imaginary circle of radius 247.5 pixels (either all clockwise or counterclockwise) while continuing to spin, resulting in each pair moving to a new quadrant of the screen. This global shift to a new location on the screen took 292 ms. Each dot pair was always oriented parallel to the midline it was crossing at the moment of crossing into a new quadrant (for example, dot pairs moving horizontally between hemifields were always oriented vertically as they crossed the vertical midline; see Figure 3.2); this prevented two targets from being within the same hemifield during between-hemifield movements (besides the moment when both dots were directly on the midline between hemifields). 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, or horizontally between the hemifields. Once the dot pairs reached their new locations, they continued spinning in place while randomly changing direction for another 2000 ms, before all dot pairs again shifted 90 degrees (either all clockwise or counterclockwise) to a new location while continuing to spin. Once the dot pairs reach their new (and final locations), all dots continued to spin while randomly changing direction for another 2000 ms before coming...
to a stop. Once the dots came to a stop, one of the two pairs containing a tracked target was cued for response by a red square frame. At this point, observers indicated which dot in the cued pair was the tracked target using a mouse click. Observers were given feedback following each trial, with the selected dot turning green when observers were correct, and red when they were incorrect. Additionally, observers were informed of their overall accuracy following each trial. Before completing the main experimental trials, observers completed 8 practice trials, which differed only in that the dot pairs remained in their original quadrants throughout the duration of the trial, instead of twice shifting globally on the screen.

As described in the previous paragraph, the dot pairs twice underwent a global shift, with each shift resulting in both the target dot pairs moving either within or between the hemifields. Each of these shifts was equally likely to be within or between the hemifields, resulting in four different conditions: two within-hemifield shifts (within-within), two between-hemifield shifts (between-between), a within-hemifield shift followed by a between-hemifield shift (within-between), or a between-hemifield shift followed by a within-hemifield shift (between-within). Importantly, the trial types separately differed in the number of times targets crossed between hemifields and the percentage of the trial targets spent within a new hemifield (see Figure 3.3). Specifically, targets did not cross between hemifields during within-within trials, crossed between hemifields twice during between-between trials, and crossed between hemifields once during both within-between and between-within trials. When considering what percentage of local rotation occurred in a new hemifield, targets spent no time in a new hemifield during within-within trials, spent 1/3 of the trial in a new hemifield during between-between trials (during the second local rotation period) and during within-between trials (during the third local rotation period), and spent 2/3 of the trial in a new hemifield during between-within trials (during
the second and third local rotation periods). Observers completed 12 trials for each of the four conditions (48 trials total), presented in a random order.

**Results**

Paired-sample t-tests revealed that observers had better accuracy for within-within trials \((M = 86.3\%, SD = 13.5\%); t(269) = 12.66, p < .001, d_z = .77)\), within-between trials \((M = 78.9\%, SD = 14.5\%); t(269) = 8.02, p < .001, d_z = .49)\), and between-within trials \((M = 78.5\%, SD = 15.4\%); t(269) = 7.68, p < .001, d_z = .47)\). Additionally, accuracy for between-between trials was worse than accuracy for within-between trials \((t(269) = 5.47, p < .001, d_z = .33)\) and between-within trials \((t(269) = 5.11, p < .001, d_z = .31)\). No significant difference in accuracy was found when comparing within-between to between-within trials \((t(269) = 0.41, p = .68, d_z = .02)\).

![Figure 3.3: Results of Experiment 1. Error bars represent within-subject SEM (Cousineau, 2005). Tracking accuracy varied as a function of the number of between-hemifield crosses (# Crosses), and did not vary as a function of the amount of time targets spent within a new hemifield (New Hemi %). Bar labels correspond to the within-within (W-W), between-between (B-B), within-between (W-B), and between-within (B-W) conditions. All conditions significantly differ from one another \((p < .001)\) except for W-B and B-W \((p = .68)\).](image)
**Experiment 1 Discussion**

Tracking performance decreased as the number of between-hemifield crosses increased, but did not vary as a function of the amount of time targets spent within a new hemifield. This result provides evidence that hemifield-specific attentional spotlights inefficiently exchange their information as targets simultaneously cross between the hemifields.

**Experiment 2: Focal vs. Divided Attention**

Despite having hemifield-limited attentional spotlights, individuals manage to successfully complete many tasks that require tracking items that move between the hemifields, (e.g., driving and playing sports). Additionally Drew et al. (2014) demonstrated that observers can successfully track a single target moving between the hemifields, in contrast to the difficulty observers had tracking multiple items moving between the hemifields in Experiment 1 and previous research (Strong & Alvarez, in prep.). How can observers’ success representing information moving between the hemifields in the Drew et al. (2014) study be reconciled with the difficulty demonstrated in other experiments?

One possible explanation for this difference is the difficulty of the tracking task used in each experiment. In the Drew et al. (2014) task, observers tracked a single target that moved between hemifields relatively slowly (2050 ms), while observers in Experiment 1 (292 ms) and the Strong & Alvarez (in prep) study (433 ms) tracked targets that moved between hemifields much more quickly. With more time to make the exchange, hemifield-limited attentional spotlights may be able to avoid the information loss that occurs when information moves more quickly between hemifields.

Another difference between the Drew et al. (2014) study and experiments finding a between-hemifield crossover cost (Experiment 1; Strong & Alvarez, in prep.) is observers’
allocation of attention between hemifields while tracking. In the Drew et al. experiment, attention was only ever deployed to one hemifield at a time as a single target was tracked, while in our experiments attention was always deployed to both hemifields as two targets were tracked. Importantly, tracking two targets in separate hemifields is no more difficult than tracking a single target in one hemifield, due to each hemifield having its own attentional spotlight (Alvarez & Cavanagh, 2005). Therefore, the success of information exchange between hemifield-limited spotlights may depend on whether attention is deployed to one hemifield or divided between the hemifields, independent of task difficulty.

Experiment 2 tested whether the transfer of information between hemifield-limited attentional spotlights depends on how attention is divided between the hemifields. Observers tracked either a single target (focal attention) or a target in each hemifield (divided attention), which shifted either within or between the hemifields. Critically, the speed at which items moved between hemifields was the same for focal and divided attention trials. Additionally, performance for tracking locally rotating targets was matched for focal and divided attention. Therefore, if information transfer between hemifields is dependent only on task difficulty, tracking targets moving between the hemifields should be equally difficult during focal and divided attention. However, if information transfer between the hemifields depends on attentional allocation, tracking targets that move between the hemifields should be more difficult when attention is divided than when it is focal.

**Method**

**Participants**

Sixteen observers (11 female, $M_{age} = 21.1$) 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 and G*Power 3.1 (Faul, Erdfelder, Lang, & Buchner, 2009), which indicated that 16 observers would be needed to achieve greater than 95% power to detect an interaction 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 x 1200 pixels), which was centered on the screen (1920 x 1200 pixels, refresh rate = 60 Hz, viewing distance = 56 cm). The midpoints of each of the four dot pairs were located 90 degrees apart along an imaginary circle of radius 12.5° 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°. Black rectangles (width = 6°) were placed at the horizontal and vertical midlines of the visual field (see Figure 3.4). A white (127 cd/m$^2$) fixation cross of diameter .8° was presented at the center of the screen.

**Procedure**

At the beginning of each trial, a pair of black dots was presented in each quadrant of the gray square background (eight dots total). Either one dot (focal attention trials) or two dots in diagonally opposite quadrants (divided attention trials) were cued as targets 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. After rotating in place for 3000 ms, all four dot pairs shifted 90 degrees along an imaginary circle of radius 12.5° (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 333 ms (20 frames of movement with a 60 Hz monitor). Each dot pair was always oriented parallel to
the midline it was crossing at the moment it reached the edge of the black rectangle on each midline (for example, dot pairs moving horizontally between hemifields were always oriented vertically when they reached the edge of the black rectangle on the vertical midline). Movement from the dot pairs’ initial locations to the edge of the black rectangles took 150 ms (9 frames). Once dots reached the edge of the black rectangles, they disappeared for 33 ms (2 frames) before reappearing on the opposite edge of the rectangle; this “teleporting” between locations appears smooth to observers (Scholl & Nevarez, 2002; Franconeri, Pylyshyn, & Scholl, 2012). After reappearing on the opposite edge of the black rectangles, dot pairs moved for 150 ms to their final locations. Once the dot pairs reached their final locations, they continued to spin in place while randomly changing direction for another 3000 ms before coming to a stop. Once the dots came to a stop, one of the two pairs containing a tracked target (divided attention) or the only pair containing a target (focal attention) was cued 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 cued pair was the tracked target using a mouse click. Observers were given feedback following 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 required to keep central fixation during all trials, which was monitored via an eye-tracking device (EyeLink 1000, SR Research, Ottawa, ON, Canada) – if observers broke fixation during tracking (>2° from fixation), the trial was terminated and restarted. Participants completed 8 alternating blocks of focal and divided attention trials (24 trials each). Whether the first block contained focal or divided attention trials was counterbalanced between observers.

Prior to the main experimental trials, a separate thresholding session (32 trials) was conducted (using the Bayesian QUEST procedure; Watson & Pelli, 1983) for focal and divided
attention trials to determine the rotational speed at which each participant could track 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) was calculated
separately for focal (\(M = 360.3\) deg/s, \(SD = 147.7\) deg/s) and divided attention (\(M = 324.9\) deg/s,
\(SD = 111.5\) deg/s); these speeds were then used during the main experimental trials. The order of
the focal and divided attention thresholding sessions was counterbalanced between observers.

\[
\begin{array}{cccc}
\text{Divided Attention} & \begin{array}{c}
\text{Within Hemifield} \\
\text{Between Hemifield}
\end{array} \\
\text{Focal Attention} & \begin{array}{c}
\text{Within Hemifield} \\
\text{Between Hemifield}
\end{array}
\end{array}
\]

\textbf{Figure 3.4}: Experiment 2 conditions. Observers used attention to track either two targets divided
between the hemifields (divided attention) or one target within a single hemifield (focal
attention). Target dots then underwent a global shift, moving to new locations either within or
between the hemifields.
Results

A 2 (attentional allocation: divided vs. focal) x 2 (trial type: within vs. between hemifield) repeated-measures ANOVA revealed a significant attentional allocation x trial type interaction ($F(1, 15) = 19.28, p < .001, d_z = 1.10$). When a target was tracked in each hemifield using divided attention, observers were better at identifying target dots after within-hemifield shifts ($M = 78.9\%, SD = 12.1\%$) than after between-hemifield shifts ($M = 62.9\%, SD = 10.0\%$; $t(15) = 5.52, p < .001, d_z = 1.38$; see Figure 3.5). When only one target was tracked within a single hemifield using focal attention, however, there was no significant difference in tracking performance for within-hemifield ($M = 78.1\%, SD = 9.9\%$) versus between-hemifield shifts ($M = 76.2\%, SD = 7.9\%$; $t(15) = 1.06, p = .30, d_z = .27$). Additionally, this ANOVA revealed significant main effects of attentional allocation ($F(1, 15) = 5.37, p = 0.04$) and trial type ($F(1, 15) = 24.20, p < .001$).

![Figure 3.5: Results of Experiment 2. Despite displaying a large cost for tracking targets moving between the hemifields during divided attention, the same observers showed no cost for tracking a single target between the hemifields during focal attention. Note that this effect cannot be explained by tracking one target being easier than tracking two targets, as no difference in performance was observed for within-hemifield movements between divided and focal attention.](image-url)
Experiment 2 Discussion

Despite displaying a large between-hemifield cost for tracking targets with divided attention, observers were able to track a single target moving between the hemifields relatively successfully, displaying a very small and statistically insignificant cost. This result suggests that hemifield-limited attentional spotlights are able to efficiently exchange their information during focal attention, but lose information when items move between the hemifields during divided attention.

Importantly, the difference in the between-hemifield cost for divided and focal attention cannot be attributed to task difficulty, despite the fact that observers tracked two targets with divided attention and only one target with focal attention. Although the speed of local rotation was separately thresholded for focal versus divided attention trials (and was slightly faster on average for focal attention), this difference was not statistically significant ($t(15) = 1.13, p = .28, d_z = .28$). Additionally, exactly half ($n = 8$) of observers ended up having a faster threshold speed for divided attention, while the other half had a faster threshold speed for focal attention; the attentional allocation x trial type interaction was present for both the half of observers with a faster focal attention threshold ($F(1, 7) = 11.38, p = 0.01$) and the half of observers with a faster divided attention threshold ($F(1, 7) = 7.63, p = 0.03$). Finally, at these speed thresholds, tracking targets moving within their original hemifields with divided attention was no more difficult than tracking a single target moving within its original hemifield with focal attention ($t(15) = 0.20, p = 0.84, d_z = .05$), consistent with previous findings of separate attentional spotlights for each hemifield (Alvarez & Cavanagh, 2005; Holcombe & Chen, 2012). Therefore, tracking targets that move between the hemifields is more difficult using divided attention because of the way
attention is allocated throughout the visual field, and not because of general differences in difficulty or target speed when tracking one versus two targets.

**General Discussion**

Tracking performance in Experiment 1 decreased as the number of times targets crossed between the hemifields increased. This result suggests that hemifield-limited attentional spotlights perform an inefficient information exchange as items simultaneously move between the hemifields. If instead hemifield-specialized spotlights continued to track their original information after items crossed between the hemifields (but did so less effectively), tracking performance in Experiment 1 would have varied with the amount of time targets spent in a new hemifield.

While Experiment 1 provided evidence for an information exchange between hemifield-specific attentional spotlights, Experiment 2 explored whether the efficiency of this exchange depends on how attention is allocated throughout the visual field. Observers displayed a large between-hemifield cost when attention was divided between hemifields, but did not show this cost when tracking a single target moving between the hemifields using focal attention, a difference not attributable to task difficulty. Therefore, although hemifield-specific attentional spotlights have difficulty coordinating an exchange of information when attention is divided between the hemifields, these same spotlights are able to transfer information between the hemifields efficiently during focal attention.

*Mechanisms of Information Transfer*

The cognitive mechanisms allowing the effective transfer of information between the hemifields during focal attention (but not divided attention) remain an open question. One
possibility is that although information is transmitted more efficiently during focal attention, the same information exchange process occurs during both focal and divided attention. Drew et al. (2014) showed that as observers track a single target moving between the hemifields using focal attention, both cerebral hemispheres temporarily represent the target as it crosses the border between hemifields. Specifically, the hemisphere receiving the incoming target begins to represent the target just before it reaches its new hemifield, while the hemisphere originally representing the target temporarily represents the target even after it reaches its new hemifield. This same process could be at work when two targets are tracked using divided attention, but be less efficient when both hemispheres must simultaneously give and receive target information. This reduced efficiency could occur either because the period of simultaneous representation by each hemisphere is reduced, or because of spatial interference between attended targets during the period of simultaneous representation (Franconeri, Jonathan, & Scimeca, 2010; Störmer, Alvarez, & Cavanagh, 2014).

Alternatively, the exchange process allowing successful information transfer during focal attention could be fundamentally different from the process that results in information loss during divided attention. For example, although information is exchanged between hemifield-limited attentional spotlights during divided attention (Experiment 1), perhaps no information exchange is necessary during focal attention. This possibility is supported by evidence that each cerebral hemisphere has the capability to deploy attention to both hemifields during focal attention, but only to the contralateral hemifield during divided attention (Battelli et al., 2009). Therefore, during focal attention both spotlights of attention may have access to target information no matter the target’s location, avoiding the need of an information exchange. This explanation is particularly notable given that target dots skipped over the vertical midline
between hemifields in Experiment 2, the critical area for information exchange found by Drew and colleagues (2014). Therefore, either the area for simultaneous representation is larger than documented by Drew and colleagues (a possibility they consider), or their result reflects a shifting in priority of which hemisphere is primarily responsible for tracking, rather than which hemisphere is exclusively representing the target.

**Future Directions**

The mechanisms of information transfer between the hemifields can be better understood by addressing two questions. The first is whether attended information is represented primarily in the contralateral hemisphere during divided attention, but in both hemispheres during focal attention. A possibility supported by a previous attentional tracking study (Battelli et al, 2009), this difference in representation could account for information transfer between hemifields being more efficient for focal attention than for divided attention. Testing this potential difference in representation should be possible using imaging or electrophysiological techniques; if such a difference exists, attended information should be equally decodable from both hemispheres during focal attention, but better decoded from the contralateral hemisphere during divided attention.

In addition to needing a better understanding of why information transfer is more efficient during focal than divided attention, the role of the border between hemifields in permitting this information exchange remains unclear. Drew and colleagues (2014) found evidence that the area surrounding the border between hemifields is critical for allowing successful information transfer, yet observers in Experiment 2 were able to track a single target moving between hemifields even though it skipped over this region. If simultaneous representation of information near the vertical midline by both cerebral hemispheres is critical
for information exchange between hemifields, then between-hemifield costs during divided attention should be larger when items skip over the border between hemifields (as in Experiment 2) than when items pass over the border between hemifields normally.

**Conclusion**

The present study provides evidence that tracking information that moves between the hemifields requires an information exchange between hemifield-limited attentional spotlights, and that the efficiency of this information exchange depends on how attention is allocated throughout the visual field. These findings demonstrate that attentional processing depends not only on the capacity of individual attentional control systems, but also on the ability of those systems to share their information with one another.
Conclusion

General Discussion

The three chapters of this dissertation demonstrate that attention is limited not only by the capacity of its individual components, but also by how those components interact with one another and with representational systems. In Chapter 1, training benefits failed to generalize between extremely similar attentional tracking tasks that shared a common attentional capacity; this result indicates that training enhanced the coordination between attentional systems and representations specific to training, and not the attentional capacity shared by the trained and untrained tasks. In Chapter 2, observers experienced difficulty using attention and working memory to maintain spatial information that moved between the hemifields, indicating that information transfer between hemifield-specific attentional control systems is necessary for effective visual processing. Finally, in Chapter 3 observers’ tracking performance decreased with an increasing number of between-hemifield crosses, consistent with an inefficient information exchange between hemifield-limited attentional spotlights during divided attention. When attention was allocated to only one hemifield, however, observers were able to successfully track a target moving between the hemifields, demonstrating that the coordination between hemifield-limited attentional spotlights depends on how attention is allocated throughout the visual field.

Importantly, although these studies provide evidence that attentional processing is limited by more than the capacity of individual attentional systems, general attentional capacity undoubtedly plays an important role in the effectiveness of cognitive functioning. This fact is evident from correlations between measures of attentional capacity and real-world outcomes (Oksama & Hyönä, 2004; Tullo, Faubert, & Bertone, 2018; Wilmer, Martini, Germine, &
Nakayama, 2016). However, as demonstrated by the results of Chapter 1 and the general inconsistency of cognitive training paradigms (Allaire et al., 2014; Simons et al., 2016), the fact a task is limited by an attentional capacity does not mean A) that the only way to improve on the task is by enhancing that attentional capacity, or B) that improvement on that task will generalize to other tasks limited by the same attentional capacity. Therefore, although the capacity of individual attentional systems may influence cognitive functioning, enhancing the capacity of those systems may not be possible through cognitive training. Furthermore, although cognitive training paradigms may improve in the future, individuals hoping to enhance or maintain their cognitive capacities are currently better off maintaining a healthy diet and exercising than participating in cognitive training paradigms (Allaire et al., 2014; Gomez-Pinilla, 2008; Gomez-Pinilla & Hillman, 2013).

Additionally, although this dissertation posits that characterizing attentional capacity alone is insufficient for improving and fully understanding attentional processing, this does not diminish the importance of understanding individual attentional systems and their limits. To the contrary, understanding various components of attention and their limitations will undoubtedly be essential for designing better training programs; without understanding different attentional processes (such as spatial versus feature-based attention; Liu, Stevens, & Carrasco, 2007; Sàenz, Buraças, & Boynton, 2003), it would be impossible to characterize or enhance those systems or their interactions. Thus, this dissertation does not claim that the study of individual attentional systems and their capacities should be abandoned; instead, it posits that individuals designing cognitive training programs should move past efforts to improve general attentional capacity. Although speculative, given the evidence that interactions between distinct cognitive
components are essential for effective attentional processing, one potential avenue for achieving generalization may be enhancing the coordination between distinct attentional processes.

**Future Directions**

Although this dissertation speculates that improving cognitive training studies may require a better understanding of how different cognitive systems interact, its experimental findings do not provide a definitive roadmap for achieving this goal. One important step towards creating better training studies will be further clarifying the nature of training-induced improvements, which likely result from changes to multiple cognitive systems and their interactions (Maniglia & Seitz, 2018). For example, the first chapter of this dissertation showed that training improves the ability of attentional mechanisms to interact with task-specific representations (rather than enhancing attentional capacity), but could not conclude whether this improved coordination was due to enhanced quality of represented information, or more efficient attentional access to the same quality of representations as before training. Future work may be able to differentiate between these possibilities in a number of ways, such as seeing whether neural signatures of sensory processing are enhanced following training even in the absence of attention (a finding that would support the possibility of enhanced representational quality). Alternatively, training paradigms could use training and outcome measures that rely on the same task-specific representations, but different attentional capacities; generalization in this case would point towards enhanced representational quality, while specificity would support enhanced access to the same quality representations.

Beyond demonstrating the need for better understanding the mechanisms of cognitive training, the studies presented in this dissertation point to a potential avenue for achieving
generalized training benefits: enhancing the coordination between separate attentional systems. Specifically, generalized training benefits may be achievable if tasks limited by the interaction of separate attentional components are trained, rather than tasks limited primarily by interactions between attention and task-specific representations. For example, the attentional tracking tasks in Chapters 2 and 3 are limited not only by the ability of hemifield-specific attentional spotlights to interact with representational content, but also by the ability of those spotlights to coordinate with one another. Therefore, it is possible that training that reduces the between-hemifield cost for one type of task (for example, multiple-object tracking) might lead to reductions in between-hemifield costs for untrained tasks that are also governed by hemifield-specific processing (e.g., spatial working memory tasks). The same possibility could be true of any task requiring the interaction of separate attentional systems, such as those for spatial attention and feature-based attention. The data presented in Chapter 2, along with previous research documenting the differences between spatial and feature-based attention, indicate that spatial attention is specific to each hemifield, while feature-based attention is deployed throughout the entire visual field (Liu, et al., 2007; Sàenz, et al., 2003). If a task were to require an interaction of spatial and feature-based attention (e.g., simultaneously performing two different multiple-object tracking tasks that vary in the features of their motion trajectories), training benefits might be expected to generalize throughout the entire visual field, unlike what was found in Chapter 1 and many previous perceptual learning studies (e.g., Karni & Sagi, 1991).

In addition to exploring whether generalization can be achieved by enhancing the coordination between distinct attentional processes, efforts to achieve generalization will also likely benefit from using cognitive modeling and deep learning. Specifically, cognitive models of training-induced learning (e.g., Solgi, Liu, & Weng, 2013) may be able to guide the design of
neurally plausible artificial neural networks that match established human patterns of training specificity and generalization (Tsodyks & Gilbert, 2004; Wenliang & Seitz, 2018). Once implemented, these networks could allow efficient testing of candidate paradigms for achieving generalization, allowing researchers to devote their time and resources to training paradigms with the highest likelihood of producing generalized learning in humans.

Conclusion

Successfully navigating complex visual environments requires prioritizing relevant information with attention. The experiments presented in this dissertation demonstrate that attentional processing is limited not only by the capacity of individual cognitive systems, but also by the ability of those systems to interact with one another efficiently. Many cognitive training paradigms have ignored this fact, failing to achieve generalized training benefits through attempts to enhance general attentional capacity. By better understanding and eventually improving the interactions between separate attentional processes, cognitive training paradigms may have a better chance of producing generalized training benefits.
Appendix A: Supplemental Information for Chapter 1

Appendix A1: Supplementary Experiment

This auxiliary experiment uses the attention operating characteristic method (Sperling & Melchner, 1978; Sperling & Dosher, 1986), which tests the extent to which two tasks use the same attentional resources. We used a very similar approach to that described in detail by Alvarez and colleagues (2005). To briefly summarize the logic of this method, there are several possible scenarios for how two tasks might interact with one another. If two tasks use completely independent resources, performing the two tasks together should be no more difficult than performing each task individually (as would be predicted for tracking objects presented in separate visual hemifields; Alvarez & Cavanagh, 2005). Alternatively, if two tasks draw continuously from the same resource, performing two tasks together should result in a decrease in performance relative to performing the tasks individually, as performing better on the first task would require participants to remove resources from (and thus perform worse on) the second task (as would be predicted for tracking two items in the same visual hemifield; Alvarez & Cavanagh, 2005). The drop in performance when completing the two tasks simultaneously can be compared to the line of mutual exclusivity, which assumes a linear tradeoff between tasks. Performance that falls on or below this line of mutual exclusivity indicates that two tasks draw upon the same attentional capacity, while performance that falls above this line indicates that the tasks use at least partially independent resources (a pattern that has been found for simultaneously performing a search and tracking task, as well as for simultaneously performing a tracking and auditory task; Alvarez et al., 2005). Points that fall below the line of mutual exclusivity are expected when tasks have steep performance-resource functions (i.e., when you cannot perform well unless you give the task a lot of resources; see Alvarez et al., 2005), such that dividing resources between two task leads to poor performance on both.

In our primary training experiment, we tested for transfer 1) between the upper and lower visual fields, 2) between dot and pinwheel tracking, and 3) between both these factors at the same time. To test A) whether items in the upper vs. lower visual field draw upon the same capacity and B) whether the dot and pinwheel tasks draw upon the same capacity, in this supplementary analysis we performed three experiments testing whether 1) dots in the upper visual field and dots in the lower visual field draw continuously from the same capacity, 2) pinwheels in the upper visual field and pinwheels in the lower visual field draw continuously from the same capacity, and 3) whether dots and pinwheels draw continuously from the same capacity.

Each experiment followed the procedure used by Alvarez et al. (2005). In each of the three experiments, 80% speed thresholds were calculated separately for successfully tracking two targets in the upper and lower quadrant of the same hemifield (either 1) dots in both quadrants, 2) pinwheels in both quadrants, or 3) dots in one quadrant and pinwheels in the other). Within each quadrant, stimuli were identical to those used in the primary training experiment. Next, participants completed 5 conditions that were perceptually identical, but required differential attentional allocation: 1) track targets only in the upper visual field (top only), 2) track targets only in the lower visual field (bottom only), 3) track targets in both the upper and lower visual fields, but prioritize targets in the upper visual field (priority top), 4) track targets in both the upper and lower visual fields, but prioritize targets in the lower visual field (priority bottom), 5)
track targets in both the upper and lower visual fields, and prioritize all targets equally (priority equal). For conditions 3-5 (where tracking occurred simultaneously in both the upper and lower visual field), we separately scored performance in the upper and lower visual fields relative to tracking performance for each visual field individually (conditions 1-2), using the formula: normalized score = [(dual task accuracy – chance)/(single task accuracy – chance)] * 100. For example, for both the dot and pinwheel task (where chance accuracy is 50% when identifying 2/4 targets), if tracking performance in the upper visual field for dots was found to be 90% when tracking only in the upper visual field, but only 70% when tracking in both visual fields with equal priority, the normalized score for dots in the upper visual field in the equal priority condition would be [(70 – 50)/(90 – 50)]*100 = 50.

**Results**

Reported means refer to distance from the mutual exclusivity line. A negative mean refers to performance falling below the mutual exclusivity line, while a positive mean refers to performance falling above the mutual exclusivity line. Error bars represent within-subject SEM (Cousineau, 2005). Eight observers participated in each of the three experiments below.

**Experiment A1A: Dot Tracking in Both the Upper and Lower Visual Field (N = 8)**

The figure illustrates the normalized performance for each condition. The data points for priority top, priority equal, and priority bottom are shown on the graph.

**Figure A1A:** Performance was not significantly different than the mutual exclusivity line for either the priority top ($M = -0.09, SD = 0.15, t(7) = 1.72, p = .13$) or the priority bottom ($M = 0.04, SD = 0.12, t(7) = 0.98, p = .36$) conditions. However, performance for the priority equal condition was significantly below the mutual exclusivity line ($M = -0.26, SD = 0.15, t(7) = 4.66, p = .002$). All three points fell on or below the mutual exclusivity line, indicating that tracking dots in the upper visual field requires the same attentional capacity as tracking dots in the lower visual field.
**Experiment A1B**: Pinwheel Tracking in Both the Upper and Lower Visual Field (N = 8)

Figure A1B: Performance was not significantly different than the mutual exclusivity line for the priority bottom condition ($M = -0.03$, $SD = 0.20$, $t(7) = 0.46$, $p = 0.66$). However, performance for both the priority top ($M = -0.20$, $SD = 0.21$, $t(7) = 2.66$, $p = 0.03$) and the priority equal ($M = -0.36$, $SD = 0.26$, $t(7) = 3.84$, $p = 0.006$) conditions was significantly below the mutual exclusivity line. Once again, all three points fell on or below the mutual exclusivity line, indicating that tracking pinwheels in the upper visual field requires the same attentional capacity as tracking pinwheels in the lower visual field. Furthermore, a mixed factors ANOVA predicting distance from the line of mutual exclusivity by condition (priority top, priority equal, priority bottom) and experiment group (dot task, pinwheel task) revealed an insignificant main effect of group ($F(1, 14) = 1.69$, $p = 0.22$) and an insignificant group x condition interaction ($F(2, 28) = 0.057$, $p = 0.94$), indicating similar mutual exclusivity between dots in the upper vs. lower visual field and pinwheels in the upper vs. lower visual field.

**Experiment A1C**: Simultaneous Dot and Pinwheel Tracking (N = 8)

This experiment had the same setup as the previous two, except participants always had dots in one visual field and pinwheels in the other (counterbalanced across participants). Therefore, we refer to the conditions as 1) priority dot, 2) priority equal, and 3) priority pinwheel.
Although performance was numerically below the mutual exclusivity line for all three conditions, the priority pinwheel ($M = -.03$, $SD = .20$, $t(7) = 0.30$, $p = .77$), priority dot ($M = -.10$, $SD = .14$, $t(7) = 2.04$, $p = .08$), and the priority equal ($M = -.16$, $SD = .21$, $t(7) = 2.20$, $p = .06$) failed to deviate significantly from the mutual exclusivity line. However, again all three points fell on or below the mutual exclusivity line, suggesting that tracking pinwheels requires the same attentional capacity as tracking dots. Furthermore, a one-way ANOVA comparing the distance of the priority equal condition from the line of mutual exclusivity across the three experiments found no reliable differences ($F(2,21) = 1.67$, $p = .21$), suggesting that tracking dots versus pinwheels in two different locations is as mutually exclusive as tracking either dots or pinwheels in two different locations.

References:


Appendix A2: Staircase procedures

A: General Procedures:
- Speeds for each motion type/location task combination (e.g., dots in the upper left quadrant) were determined using two independent, interleaved staircases. For each staircase, each correct trial (correctly identifying both targets) resulted in the staircase speed increasing by the current step size. Each time a staircase had two consecutive incorrect trials occur, the staircase speed decreased by 3X the current step size. A reversal trial occurred when either 1) a correct trial occurred after any two consecutive incorrect trials or 2) two incorrect trials occurred following any correct trial. The mean of each staircase’s final four reversals was designated at the overall staircase speed. The mean of the two overall staircase speeds was designated as the threshold speed for each motion type/location combination.

B: Assessment Day Staircase Parameters
- One staircase (SC1) always began at half the speed of the second staircase (SC2). Each staircase had a step size of 3X the final step size until 4 reversals occurred. The step size was then set at 2X the final step size until two more reversals occurred (6 total). After 6 reversals, each staircase was set to its final step size until 10 reversals were reached. Staircases for all task types were randomly interleaved, and selected based on a weighted probability of the number of remaining reversals until completion.
  - Dots
    - Starting Speeds: SC1 = 8.923 deg/s, SC2 = 17.846 deg/s
    - Final Step Size = 0.892 deg/s
    - Minimum Speed = 1.78 deg/s
  - Pinwheels
    - Starting Speeds: SC1 = 150 deg/s, SC2 = 300 deg/s
    - Final Step Size = 10 deg/s
    - Minimum Speed = 50 deg/s

- Example Staircase (assessment session, pinwheel top-right quadrant. Final four reversals for each staircases are marked):

![Example Staircase Graph]
C: Training Day Staircase Parameters
- Two independent randomly interleaved staircases were also used for the training sessions. Staircases ran for 55 minutes regardless of number of reversals. SC1 began a designated amount below the previous day’s threshold speed, while SC2 began a designated amount above (see below). For the first training session (day 3), the baseline assessment speed for the training task (from day 2) was used as the previous day’s threshold speed. For the rest of the training sessions (days 4-8), the mean of each staircase’s final four reversals was used to calculate threshold speed in the same way as in the assessment sessions (described above). The step size was constant throughout, and the same as the final step size used in the assessment sessions.
  - Dots
    - Starting Speeds: SC1 = previous day’s threshold – 4.46 deg/s, SC2 = previous day’s threshold + 4.46 deg/s
    - Step Size = 0.892 deg/s
    - Minimum Speed = 1.78 deg/s
  - Pinwheels
    - Starting Speeds: previous day’s threshold – 75 deg/s, SC2 = previous day’s threshold + 75 deg/s
    - Final Step Size = 10 deg/s
    - Minimum Speed = 50 deg/s
- Example Staircase (training session, pinwheel top-right quadrant. Final four reversals for each staircases are marked):
D: Practice Day Staircase Parameters
- On practice days, staircases were run for 30 minutes, regardless of number of reversals. Procedure for practice day was similar to the assessment day, except with different starting speeds and step sizes. The step size also remained constant throughout the practice session.
  o Dots
    ▪ Starting Speeds: SC1 = 5.354 deg/s, SC2 = 10.707 deg/s
    ▪ Step Size = 0.446 deg/s
    ▪ Minimum Speed = 1.78 deg/s
  o Pinwheels
    ▪ Starting Speeds: SC1 = 100 deg/s, SC2 = 200 deg/s
    ▪ Step Size = 5 deg/s
    ▪ Minimum Speed = 50 deg/s
Figure A3: Training results if subject replacement had not occurred. The Trained condition still showed significantly greater improvement than all other conditions (including control), while all transfer conditions (New Motion, New Location, and Both New) all failed to differ significantly from control. Improvement for all conditions was still significantly greater than 0. The only change in significance was that the New Location condition was not significantly different than control before subject replacement occurred, but was significantly greater in our main report. The New Location was still significantly greater than the Both New condition (when aggregated across dot and pinwheel training), however, consistent with our claim that partially shared features between training and outcome measures may allow limited generalization of training benefits.
Appendix A4: Condition Means and Standard Deviations

Table A4A:

*Mean and Standard Deviation of Percent Improvement by Training Condition*

<table>
<thead>
<tr>
<th></th>
<th>Dot Training</th>
<th>Pinwheel Training</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M</td>
<td>SD</td>
</tr>
<tr>
<td>Trained</td>
<td>59.6</td>
<td>33.9</td>
</tr>
<tr>
<td>New Motion</td>
<td>26.7</td>
<td>33.9</td>
</tr>
<tr>
<td>New Location</td>
<td>34.4</td>
<td>22.8</td>
</tr>
<tr>
<td>Both New</td>
<td>18.7</td>
<td>29.5</td>
</tr>
</tbody>
</table>

Table A4B:

*Mean and Standard Deviation of Control Condition*

<table>
<thead>
<tr>
<th></th>
<th>M</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>17.4</td>
<td>20.3</td>
</tr>
</tbody>
</table>
Appendix A5: Individual Subject Distributions of Learning and Transfer

A

B
Figure A5: Individual Subject Distributions of Learning and Transfer. Each figure plots individual subject improvement for the trained task versus improvement for one of the untrained transfer tasks (A: new motion, B: new location, C: both new). Within each plot, each data point represents a subject in either the dot training (black circles) or pinwheel training (red circles) group. Points that fall within the white region indicate greater gains for the trained condition than the untrained transfer condition, while points in the gray indicate the opposite. Points falling on the line between the white and gray regions indicate equal improvement for the training and untrained transfer condition.
Appendix A6: Mixed Effects Analysis Code

The original R file can be downloaded at: https://scorsese.wjh.harvard.edu/turk/experiments/rws/Misc/Exp3_Mixed_Effects.R

```r
# load packages
if (!require("lme4")) install.packages("lme4"); require("lme4")
if (!require("lmerTest")) install.packages("lmerTest"); require("lmerTest")
if (!require("effects")) install.packages("effects"); require("effects") # for plotting

# import data
file_link = 'https://scorsese.wjh.harvard.edu/turk/experiments/rws/Misc/MOT_Training_Data.csv'
data_matrix = read.table(file_link, header = TRUE, sep = ",", )

#--- data_matrix (and data_matrix_noControl) explanation
# id = subject number
# training_group = which training group the participant was part of: Exp1 (dot training), Exp2 (pw training), or Exp3 (control)
# did_training = During training period, whether participants did training: Yes (Exp 1/2) or No (Exp 3)
# left_right = visual field of task: left or right
# motion = motion type of task: Dot or PW
# top_bottom = visual field of task: top or bottom
# pre = baseline speed threshold (in degrees of visual angle/s for Dot, in degrees/s of rotation for PW)
# post = post-training speed threshold (in degrees of visual angle/s for Dot, in degrees/s of rotation for PW)
# improvement = 100*{(post - pre)/pre} - outcome measure of interest
# condition = condition of task
# - trained = trained task
# - new motion = same location as training task, but different motion
# - new location = same motion as training task, but different location
# - both new = both location and motion are different from training task
# - control = there was no training task (control participants)

# create subject id factor levels
data_matrix$id = factor(data_matrix$id)

# sort factor levels for condition to be 1) Trained, 2) New Motion, 3) New Location, 4) Both New, 5) Control (for plotting)
data_matrix$condition = factor(data_matrix$condition, levels(data_matrix$condition)[c(5,4,3,1,2)])

# make a matrix of training (non-control) subjects only for first part of analysis
data_matrix_noControl = data_matrix[data_matrix$did_training == "Yes",]

# reference conditions for statistical tests (Exp 1/2 = trained, Exp 3 = control)
data_matrix_noControl$condition <- relevel(factor(data_matrix_noControl$condition), ref = "trained")
data_matrix$condition <- relevel(factor(data_matrix$condition), ref = "control")
```
#---------------- Model Comparison to Test For Differences Between Exp 1 & Exp 2
#starting with fully saturated model with all possible fixed effects
m0 <- lmer(improvement ~ condition * training_group * top_bottom * left_right + (1 | id), data = data_matrix_noControl)
summary(m0)
#use step function in lmerTest to perform backward elimination of non-significant factors
m0_reduced = step(m0)
m0_reduced
#--> simplified model is: improvement ~ condition + (1 | id)...other fixed effects and interactions do not provide a better fit

#Model 1: DV = improvement | Fixed Effect: condition | Random Intercept: id
ml <- lmer(improvement ~ condition + (1 | id), data = data_matrix_noControl)
summary(ml)
ml.eff <- Effect("condition", ml)
plot(ml.eff)
#Comparison of fixed effects (relative to trained condition):
#                         Estimate    Std.Error   df      t value   Pr(>|t|)
#(Intercept)               57.918      4.577    89.490    12.654    < 2e-16
#  conditionnew motion     -32.059      5.184    93.000    -6.184    1.65e-08
#  conditionnew location   -23.182      5.184    93.000    -4.472    2.19e-05
#  conditionboth new       -40.306      5.184    93.000    -7.774    1.00e-11
#----> improvement for trained condition significantly greater (p < .05) than other three conditions (new motion, new location, both new)

#Model 2: DV = improvement | Fixed Effects: condition, training_group | Random Intercept: id
#seeing if adding training_group as a fixed effect results in a better model
m2 <- lmer(improvement ~ condition*training_group + (1 | id), data = data_matrix_noControl)
summary(m2)
m2.eff <- Effect(c('condition','training_group'), m2)
plot(m2.eff)

#Model Comparison: ml vs m2
anova(ml, m2) #p = .9939
#Model 2 is not significantly better than Model 1 (Model 1 is actually better (although not significantly), with a lower AIC)
#therefore, no significant differences in improvement between experiments 1 and 2

#---------------- Now Test For Differences Between Exp 1+2 vs Exp 3
#starting with fully saturated model with all possible fixed effects
m3_sat <- lmer(improvement ~ condition * motion * top_bottom * left_right + (1 | id), data = data_matrix)
summary(m3_sat)
#use step function in lmerTest to perform backward elimination of non-significant factors
m3_reduced = step(m3_sat)
m3_reduced
# Model 3: DV = improvement | Fixed Effect: condition | Random Intercept: id
m3 <- lmer(improvement ~ condition + (1 | id), data = data_matrix)
summary(m3)

m3.eff <- Effect("condition", m3)
plot(m3.eff)

# Comparison of fixed effects (relative to control condition):
#                     Estimate    Std. Error      df     t value     Pr(>|t|)
# (Intercept)           17.3736     4.7999     46.0000     3.620     0.000732
# conditiontrained      40.5445     6.6900     75.0200     6.060     5.03e-08
# conditionnew motion    8.4851     6.6900     75.0200     1.268     0.208608
# conditionnew location 17.3623     6.6900     75.0200     2.595     0.011365
# conditionboth new      0.2387     6.6900     75.0200     0.036     0.971637

#----> improvement for trained and new location significantly greater (p < .05) than control

# Model 3b: DV = improvement | Fixed Effects: condition, motion, condition*motion | Random Intercept: id
m3b <- lmer(improvement ~ condition*motion + (1 | id), data = data_matrix)
summary(m3b)
m3b.eff <- Effect(c('condition','motion'), m3b)
plot(m3b.eff)

anova(m3, m3b)

#----> Model 3b is not significantly better than Model 3 (Model 3 is actually better (although not significantly), with a lower AIC)
#----> therefore, improvement did not vary across conditions differently between dot movement and pinwheel movement
Appendix A7: Dot Training and Pinwheel Training Learning Curves

A: Dot Training

B: Pinwheel Training

Figure A7: Speed Thresholds and Learning Curve for Dot Training (A) and Pinwheel Training (B). A different staircase procedure was used for the training days (days 3-8) than was used during the two assessment days (days 2 and 9). Error bars represent SEM. Note that the control condition in each of these graphs reflects the same data (as well as the same data presented in the learning curve in the manuscript), while the other four conditions represent data specific to dot training (A) or pinwheel training (B) subjects.
Appendix A8: Correlation of Dot and Pinwheel Baselines Speed Thresholds

Figure A8: Correlation of baseline dot and pinwheel speeds for participants across all three experiments (N = 48). Each participant received two baseline speeds for each motion type (one in the upper visual field and one in the lower visual field). For each participant, the two baseline speeds for each motion type were averaged, producing a single dot speed and pinwheel speed used to compute this correlation.
Appendix B: Supplemental Information for Chapter 2

Supplement B1: Mirror-image confusion analysis for spatial working memory

Figure B1: Results of mirror-image confusion analysis for Experiment 2A. Observers performed better for within-hemifield movements than between hemifield movements no matter if the dots in the cued grid were originally positioned parallel, perpendicular, or oblique to the direction of the grid’s movement. Error bars represent within-subject SEM (Cousineau, 2005).

We interpreted the between-hemifield crossover cost in Experiment 2A as evidence of hemifield-specific control of spatial working memory. A possible alternative explanation is that maintaining a representation in one hemifield automatically generates a laterally mirrored representation in the opposite hemifield, due to inter-hemispheric connections between the laterally symmetric hemispheres of the brain (Rollenhagen & Olson, 2000). For example,
consider a 2x2 grid (like those in Experiment 2A) appearing in the bottom-left quadrant of the screen with dots in its upper-left and lower-left cells. If maintaining this grid in working memory resulted in the activation of a laterally-mirrored right-hemifield representation (of a grid with dots in its upper-right and lower-right cells), interference between these two representations might occur when the grid moved between the hemifields, but would not occur when the grid moved within its original hemifield. If this explanation is responsible for the between-hemifield crossover cost in Experiment 2A, the crossover cost should not occur for grids that are laterally symmetric (e.g., a grid with dots in its upper-left and upper-right cells), as the laterally-mirrored representation would be identical to the original representation.

To test whether a laterally-mirrored representation or target information produced the between-hemifield crossover cost, we grouped trials into whether the original layout of dots in the cued grid was A) parallel to the direction of movement (vertically aligned dots in a grid moving vertically within-hemifield, or horizontally aligned dots in a grid moving horizontal between-hemifield), B) perpendicular to the direction of movement (vertically aligned dots in a grid moving horizontally between-hemifield, or horizontally aligned dots in a grid moving vertically within-hemifield), or C) oblique to the direction of movement (diagonally aligned dots in a grid moving either vertically within-hemifield or horizontally between-hemifield; see Figure B1 for examples). Critically, trials where dots are aligned parallel to the direction of motion would not have a conflicting representation during between-hemifield movements, as the laterally mirrored representation would be identical to the original representation. Trials where the layout was perpendicular or oblique to the direction of movement would have different laterally-mirrored representations, and therefore potential conflict during between-hemifield movements. Therefore, is the crossover cost is the result of lateral mirror-confusion during
between hemifield movements, a crossover cost should be found for perpendicular and oblique trials, but not for parallel trials.

A separate dependent-measures t-test for each layout type revealed that a between-hemifield crossover cost occurred for all three types of trials (parallel: $p = .02$; perpendicular: $p < .001$; oblique: $p = .007$), indicating that differences between lateral and vertical mirror confusion cannot be the sole explanation of the between-hemifield crossover cost. Although the accuracy difference between within-hemifield and between-hemifield movements was numerically larger for perpendicular movements than for parallel and oblique movements, these differences were not significant. A significant difference between the crossover cost for parallel trials and perpendicular trials would have suggested that lateral mirror-image confusion contributes to the crossover cost for spatial working memory. However, even if this had been the case, the significant difference between within- and between-hemifield movements for parallel trials still would have indicated that mirror-confusion cannot be the sole cause of the between-hemifield crossover cost for spatial working memory.
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