



Test of a dynamic neural field model: spatial working memory is biased away from distractors

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Abstract

Attention facilitates the encoding (e.g., Awh, Anllo-Vento, & Hillyard, *J Cognit Neurosci* 12(5), 840–847, 2000) and maintenance of locations in spatial working memory (Awh, Vogel, & Oh, *Atten, Percept Psychophys* 78(4), 1043–1063, 2006). When individuals shift their attention during the maintenance period of a spatial working memory task, their memory of a target location tends to be biased in the direction of the attentional shift (Johnson & Spencer, 2016). Dynamic field theory predicts that in certain conditions, inhibitory mechanisms will result in biases away from distractors presented during the maintenance period of the task. Specifically, dynamic field theory predicts that memory responses will be biased toward distractors that are near the target location and biased away from distractors that are farther from the target location. In two experiments, the current study tested adults in a spatial memory task that required memorization of a single target location. On a subset of trials, a distractor appeared during the memory delay at different distances and directions from the target location. In contrast to the prediction, memory responses were biased away from distractors that were near the target location and not biased by distractors that were far from the target location, providing challenges for, dynamic field theory and other theories of spatial working memory.

Introduction

A large body of behavioral and neuroimaging work has shown a close connection between attention and spatial working memory (SWM). For example, selectively attending to a location facilitates the encoding of that location in SWM (e.g., Awh, Anllo-Vento, & Hillyard, 2000). Selective attention, however, is also involved in the maintenance of locations in SWM (see Awh, Vogel, & Oh, 2006, for a review). Smyth and Scholey (1994) propose that covert shifts of endogenous spatial selective attention act as a rehearsal mechanism in SWM. Awh and colleagues propose that adults keep a spotlight of attention focused on the remembered location (Awh et al., 1999; Awh, Jonides, & Reuter-Lorenz, 1998; Awh & Jonides, 2001), such that when adults shift this spotlight, the accuracy of their memory decreases (Awh, Jonides, & Reuter-Lorenz, 1998). Similarly, adults increase directed attention to a remembered location when

they know that distractors may appear during the maintenance period (Awh, Matsukura, & Serences, 2003).

Recent research has examined whether SWM may actually be biased, or distorted, by shifts of attention rather than just disrupted. During the maintenance period of a spatial recall task, Van der Stigchel, Merten, Meeter and Theeuwes (2007) presented sudden onsets to determine whether attention shifts during the maintenance period would distort SWM. Sudden onsets are stimuli that automatically capture attention (e.g., Schreij, Owens, & Theeuwes, 2008). Van der Stigchel and colleagues found that when the sudden onset was near the target location that was being maintained in memory, memory responses were biased toward the location of the sudden onset. In contrast, when a sudden onset was far from the target location, memory responses were not biased. Herwig, Beisert, and Schneider (2010) found similar results in a spatial memory task where the response was a saccade directed toward the memorized location.

Recently Johnson and Spencer (2016) proposed another explanation of these distortions in SWM. Johnson and Spencer proposed that, although spatial selective attention interacts with SWM, maintaining a spotlight of attention on a location is not necessary for maintaining the location in memory. Specifically, Johnson and Spencer proposed that

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a shift of attention during the maintenance period might induce the memory representation to drift toward the locus of attention rather than cause a disruption of the representation. Johnson and Spencer based their hypotheses on a neural network model, dynamic field theory (DFT), of SWM. This model uses dynamic neural fields to model SWM (e.g., Johnson, Spencer, & Schöner, 2009). In this DFT model there is no separate attention mechanism. Rather biases emerge from the interaction of populations of neurons.

Based on the model, Johnson and Spencer (2016) proposed that when participants were required to shift their attention to a small circle during the delay of a spatial recall task, their spatial memory responses would be biased toward the locus of attention, but when participants could ignore the circle, they would not be biased toward the location. To test this hypothesis, participants completed several conditions, including a shifting-attention and a shifting-control condition. In the shifting-attention condition participants had to shift their attention to a small circle presented during the memory delay to complete a color discrimination task. In the shifting-control condition, the colored circle appeared during the delay, but participants could ignore it. Memory responses were biased toward the locus of attention, the colored circle, in the shifting-attention condition, but were not biased in the shifting-control condition.

Children show a different pattern of memory biases than adults. Schutte, Keiser, and Beattie (2017) tested children in a spatial recall task similar to the shifting-control condition from Johnson and Spencer (2016). Specifically, children saw a target appear on a large, touchscreen monitor, then disappear. On a subset of the trials, a yellow distractor dot appeared during the retention interval. The distractor could be either close to or far from the target location. The distractor remained on for 1000 ms. Unlike the adults in Johnson and Spencer (2016), the memory responses of the 6-year-olds were biased away from the distractor when it was near the memorized location. The reason for this difference between the responses of adults and 6-year-olds is unclear. The difference in memory biases may be a developmental difference, or differences in the task may cause the difference in biases.

Adults show repulsion in certain spatial tasks. For example, when tracking multiple targets and distractors and then reporting their final locations, adults report distractors as being farther apart from each other than they actually are (Liverence & Scholl, 2011). Liverence and Scholl label this an inhibitory expansion effect. In addition, location memory responses of adults are repulsed from nearby landmarks (Schmidt, Werner, & Diedrichsen, 2003) and from the symmetry axis of the task space (Schmidt, Werner, & Diedrichsen, 2003; Spencer & Hund, 2002). In all of these cases, however, memory is repulsed from a distractor, landmark or reference axis that is present during encoding as

well as during maintenance and recall. Repulsion from a distractor present only during the maintenance period has not been found in adults. One possible reason for the lack of repulsion effects in adult studies is the short length of time distractors are present.

Schutte, Keiser, and Beattie (2017) suggested that the relatively long length of time the distractor was present might have led to children's memory responses being repulsed from distractors in a manner that is similar to memory biases away from nearby landmarks (Schmidt, Werner, & Diedrichsen, 2003). In Schutte, Keiser, and Beattie, distractors were present for at least 1000 ms. In the previous work in adults, the distractor was presented for 500 ms (Johnson & Spencer, 2016) or less (Herwig, Beisert, & Schneider, 2010; Van der Stigchel et al., 2007). In the DFT model, repulsion from a distractor occurs as the result of inhibition centered at the location of the distractor input, but inhibition takes times to build. In the next section we examine whether the inhibitory component of DFT can result in a bias away from a distractor by presenting a distractor input to the model for 1000 ms. We present an overview of the DFT model and simulations of the model that confirm memory responses in the model are biased away from distractors under certain conditions. We then generate the predictions that we tested in an empirical experiment.

Dynamic field theory

DFT is a dynamic systems model that uses dynamic neural fields (Amari, 1989; Amari & Arbib, 1977) to simulate behavior. This model is one of a class of neural network models that use the sustained activation of neurons arranged topographically to model working memory (e.g., Almeida, Barbosa, & Compte, 2015; Compte et al., 2000; Schneegans & Bays, 2018). In this paper, we use the DFT model and parameters used by Schutte and Spencer (2009) to model SWM performance in a task similar to the one used by Schutte and Spencer. In this SWM model, activation at the target location is sustained in working memory through excitatory connections between neurons that code for similar locations and broader inhibition from a field of inhibitory neurons. The combination of excitatory and inhibitory connections results in a Mexican-hat shaped interaction function.

A simulation of the SWM model is shown in Fig. 1. This model uses the three layers of neurons and the adult parameter settings used by Schutte and Spencer (2009) to model SWM performance in adults. Johnson and Spencer (2016) include an additional layer that codes both a color dimension and a spatial dimension to account for performance in the color discrimination task. Given that the task in this study does not include a color discrimination task, we simplify

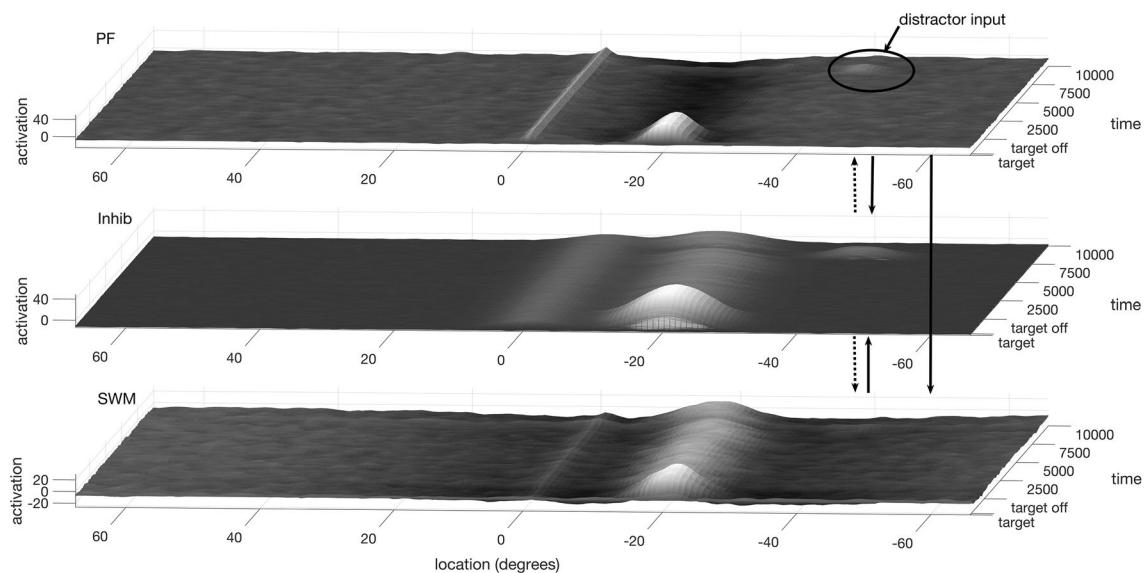


Fig. 1 Simulation of the dynamic field theory (DFT) model of SWM. Layers represent the perceptual field (PF), inhibitory field (Inhib), and excitatory working memory field (SWM). Arrows represent interaction between fields. Solid arrows represent excitatory connections and dashed arrows represent inhibitory connections. In each field, loca-

tion in degrees is represented along the x -axis (with midline symmetry axis at 0°), activation along the y -axis, and time along the z -axis. The trial begins at the front of the figure and moves toward the back. Distractor input turned on at 7500 ms and remained on for 1000 ms. See text for additional details

the model by not including the additional layer. Figure 1 displays activation in each layer for one trial of a simple SWM task (Schutte, Keiser, & Beattie, 2009). The three layers have location on the x -axis in degrees, activation on the y -axis, and time in ms on the z -axis with the beginning of the trial at the front of the graph. The top layer is the Perceptual Field (PF). This field codes any perceptual input to the model. When activation at a location is above 0, this layer sends excitation to the corresponding locations in the other two fields. Activation in this layer is not maintained when the input is no longer present. The middle layer is the Inhibitory Field (Inhib), which receives excitation from the other two fields, and sends inhibition back to them. For example, the result of this inhibition can be seen in the “troughs” of lower activation in the perceptual layer. The bottom layer is the spatial working memory (SWM) field, which maintains locations in memory through sustained activation.

In the task, a target is presented on an otherwise blank computer screen for 2000 ms. The subsequent memory delay lasts for 10,000 ms, and, during the delay, a distractor appears for 1000 ms. Targets are presented on a semicircle centered at the bottom, center of the monitor (see Fig. 4). The model simulates directional responses in degrees. In Fig. 1 the target is at -20° and the distractor input is at -40° . At the start of a trial, there is low-level activation at 0° in PF and SWM. This activation is associated with the midline symmetry axis, an axis used as a reference axis in spatial memory (e.g., Simmering, Spencer, & Schöner,

2006; Schutte, Simmering, & Ortmann, 2011). When a target appears, a strong Gaussian input at the target location builds a peak in PF, which passes activation to SWM (see solid arrow from PF to SWM). SWM has strong recurrent excitatory connections that result in a self-sustaining peak at the target location after the target input turns off. In contrast, the recurrent excitatory connections in PF are weaker than the connections in SWM so the target activation dies away when target input turns off. The low-level activation associated with the midline reference axis remains, because the axis is always perceptually available. Note that both PF and SWM send activation to the inhibitory field (see solid arrows in Fig. 1). The inhibitory field then sends inhibition back to both fields (see dashed arrows in Fig. 1). The inhibition sent to SWM is broader than the excitatory activation, resulting in lower activation levels around peaks of activation, i.e., a Mexican hat interaction function. This inhibition keeps peaks of activation stable (see Appendix for equations and the full set of parameters).

During the memory delay, inhibition associated with the midline reference axis causes the peak in SWM to drift away from midline. At 7500 ms, the distractor input turns on and remains on for 1000 ms. The distractor input creates a small peak in PF, but it is not strong enough to create a peak in SWM. The peak in PF is strong enough, however, to feed excitatory input into SWM and Inhib while the distractor input is present. Thus, the distractor input can influence the target peak in SWM. If the peak in SWM overlaps with the

excitatory input from PF, the peak will move toward the distractor, but if the peak overlaps with the inhibition associated with the distractor, but not the excitatory input, the target peak moves away from the distractor location (Fig. 1).

Repulsion from a distractor is shown more clearly in the simulation in Fig. 2a. This figure has the same three layers as in Fig. 1 with activation on the y-axis and location in degrees on the x-axis. Instead of plotting continuous time, the each graph shows the state of the field at three time points. The first time point is 100 ms before the distractor input turns on

(dashed, light gray line). At the start of the trial the target input was centered at -20° , but the peak in the SWM field has clearly drifted away from the midline input at 0° . The second time point is right before the distractor input turns off (solid black line). As can be seen in the figure, the peak in SWM has been influenced by the inhibition associated with the distractor input. The peak is smaller overall, but, importantly, it has also been “pushed” back toward 0° . The last time point is the end of the delay (dark gray, dot-dash line). The distractor input is no longer present, so the peak

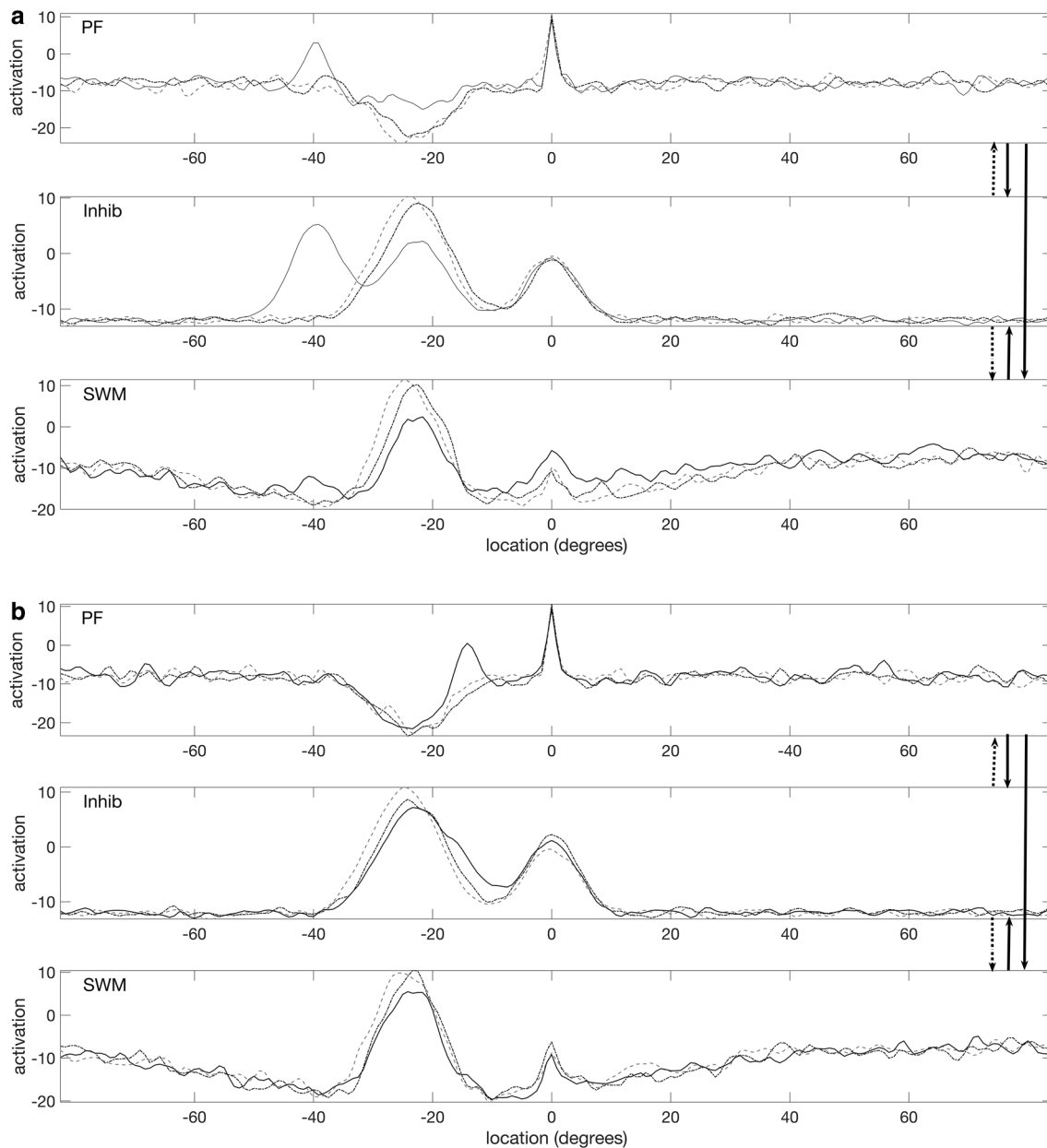


Fig. 2 Two simulations of the DFT model with location on the x-axis and activation on the y-axis. For each field (PF, Inhib, and SWM), activation at three time points is shown: 100 ms before the distractor input turns on (dashed, light gray line), right before the distractor

input turns off (solid black line), and at the end of the delay (dot-dash, dark gray line). In both simulations, the target is at -20° , and in **a** the distractor is at -40° and in **b** the distractor is at 15°

in SWM is taller, but it is still closer to 0° than it was prior to the distractor input. Figure 2b is a simulation that shows a similar pattern of drift, but in this simulation, the distractor input is at 15° , i.e., 5° from the target in the direction of midline. The peak in SWM has once again drifted away from the midline input during the first part of the delay (dashed, light gray line), but, in this case, when the distractor input is present the peak goes toward the distractor input due to the excitatory input being so close to the peak. As a result, the peak is once again closer to midline at the end of the trial (dark gray, dot-dash line) (Fig. 2b).

In the simulations in Figs. 1 and 2, the distractor input is a Gaussian with a width of 3° , the same as the target input, and the distractor strength was set to 12. To confirm that the peak in the memory field is biased by distractor input, we ran a series of simulations for targets that were 20° and 40° from the midline symmetry axis. For each simulation, there was either no distractor or a distractor 5° , 12.5° , or 20° from the target. Distractors could be on either side of the target. The distractor width was set to 3° , and we used four different distractor strengths: 9, 10, 11, or 12. Exploration of different strength parameters determined that a distractor strength of 13 or more killed the self-sustained peak in the SWM field on more than 25% of the trials. Limiting the strength of the distractor is a simplification that mirrors the effect of using a color-space input field, like that used by Johnson and Spencer (2016), which limits the strength of inputs to PF that are not the same color as the target. We ran 150 simulations for each target, distractor location, and distractor strength combination. The difference between mean constant error with no distractor and mean constant error for each distractor location and strength is shown in Fig. 3. Distractors between the target location and the midline reference axis input are negative (i.e., -5° , -12.5° , and -20°), and distractors that are on the opposite side of the target from midline are positive (5° , 12.5° , and 20°). The pattern of bias did not vary by target location, so these data are collapsed across target. Positive difference scores are biases away from the distractor, and negative difference scores are biases toward the distractor.

As can be seen in Fig. 3, the influence of the distractor varied depending on the location of the distractor relative to the target. When the distractor was $\pm 20^\circ$ from the target location, the peak in SWM was biased away from the distractor, although the amount of bias depended on the strength of the distractor. When the peak was 5° or -12.5° from the target location, the peak in SWM was biased toward the distractor, although, again, the amount of bias depended on the strength of the distractor. Notably, the 5° distractor did not have a significant impact on bias. During the delay, the peak in SWM drifted away from the midline axis, which is also toward the 5° distractor. Thus, when the distractor input comes in at 7500 ms, the target peak almost directly overlaps with the location of the distractor input, which results in the

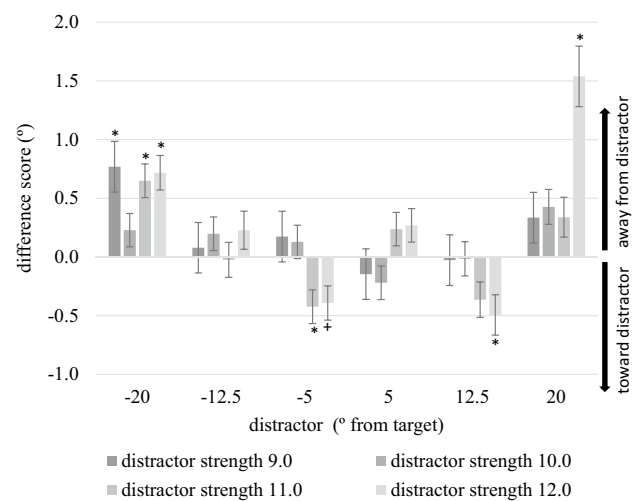


Fig. 3 Difference between the mean constant error from simulations without a distractor and with a distractor. Positive difference scores are biases away from the distractor and negative difference scores are biases toward the distractor location. Errors represent the standard error of the mean. * $p < .05$, + $p < .10$

distractor input having only a weak effect, if any, on the peak in SWM. This lack of an effect occurs for two reasons. First, distractor input into PF almost overlaps with the inhibitory trough that is the result of the inhibition associated with the peak in SWM. This inhibition results in the distractor peak in PF not being strong enough to reach zero, and, thus, very little, if any, excitation is input into SWM. Second, the distractor inhibition from the inhibitory field is close to centered with the peak in SWM, so it does not cause much, if any, repulsion from the distractor input. In contrast, the drift away from midline puts the target peak close enough to the 12.5° distractor for the strongest distractor input to cause a bias toward the distractor, and far enough from the -12.5° distractor for it to not have a consistent effect on the target peak. In other words, when the distractor is at -12.5° , the peak drifts toward the distractor on some trials and away from the distractor on other trials.

To summarize, the inhibition from the distractor influenced the peak in memory when the distractor was 20° from the target. When the distractor was closer to the target peak, the peak was either not influenced by the distractor or the excitatory input from the distractor caused the peak to drift toward the distractor location. Similar computational models have led to similar predictions. Using a similar neural field model to capture saccade deviations toward or away from a distractor, Wang, Kruijne, and Theeuwes (2012) found that, in the model, deviations toward and away from a distractor depended on the timing and location of the distractor. Similar to our simulations, when the distractor was near the target the model deviated toward the distractor, and when the distractor was farther from the target the model deviated

away from the distractor. Using a similar model, Almeida, Barbosa, and Compte (2015) predicted a comparable pattern of biases when maintaining multiple items in working memory. Specifically, simulations of their model resulted in the prediction that if two items being maintained in memory were close to each other, they would be attracted toward each other. If they were further from each other, they would be biased away from each other. They confirmed these predictions empirically. Thus, this pattern of biases is not unprecedented, although it has not been found with distractors in a memory task.

We tested adults in a spatial recall task equivalent to the task modeled by the simulations. In this task participants had to remember the location of a target on a large touchscreen, and when the computer said “go”, they used a stylus to touch the location of the target. On a subset of trials, a distractor appeared somewhere on the screen during the maintenance period. We tested two specific hypotheses generated by the simulations: (a) memory for the target location would be biased away from distractors that are farther from the target location and either not biased or biased toward distractors closer to the target, and (b) biases caused by distractors would vary depending on whether the distractor is toward or away from midline relative to the target location.

Experiment 1

Methods

Participants

One hundred twenty-seven college students (74 females, 53 males) completed the spatial recall task as part of a larger study. Participants received course credit for their participation. The study was approved by the institutional review board and was performed in accordance with the ethical standards in the 1964 Declaration of Helsinki and its later amendments. All participants provided informed consent, and reported normal or corrected-to-normal vision. As part of the larger study, participants completed the Ohio State University traumatic brain injury (TBI) identification method interview (Corrigan & Bogner, 2007; Bogner & Corrigan, 2009). Only participants who did not report a TBI (i.e., did not report a head injury with a loss of consciousness) were included in these analyses. One hundred three participants (59 females, 44 males) were included in these analyses.

Apparatus

Participants sat in front of a large 32-inch \times 18-inch (82.16 cm \times 46.28 cm) liquid crystal display (LCD) computer

monitor (Sharp, Inc.) with a resolution of 1024 \times 768 pixels. The monitor was tilted 15 degrees up from horizontal. A touchscreen overlay (Smartboard) recorded the touch of a stylus. The computer monitor was surrounded on three sides by a black curtain set 2–3 feet back from the monitor. The lights in the room were dimmed to prevent any reflections on the monitor.

Procedure

The task started with the experimenter performing a demonstration trial that was the same as test trials. Each trial began when the computer said, “Let’s look for a spaceship,” the target, a 1 cm \times 1 cm blue triangle, then appeared for 2000 ms. To avoid adding a landmark to the task space, we did not use a fixation point during the delay. Instead, the experimenter instructed the participant to look toward the top center of the monitor during the delay and reminded the participant of this if the participant appeared to be looking at the target location or the participant’s head did not appear to come up. Note that the monitor was large enough and positioned in such a way that participants usually moved their heads when they switched their gaze from the target location to the top center of the monitor. Note that during the delay participants kept their hands in their lap. Following the delay (see below), the computer said, “Go, go, go,” and the participant touched the remembered target location with a stylus. The experimenter instructed the participant that if he or she accidentally touched in an unintended location on the first touch, the participant could touch again in the correct location. If the first touch was in the correct location, the participant tapped twice in order for the trial to continue. If the participant did not touch twice, the experimenter hit a key on the keyboard to continue the trial. On a subset of trials, the distractor, a yellow dot 1 cm in diameter, appeared during the delay. The researcher instructed the participant to ignore the yellow dot. After each trial, the target was re-illuminated for 4000 ms. The participants received verbal and visual feedback from the computer based on whether he/she found the target (was within 1 cm of the center of the target), was close to the target location (was within 3 cm of the center of the target), or did not find the target.

Participants completed two practice trials followed by 84 test trials (42 trials to each target). The order of the test trials was randomized. One target location was 40° to the right of the midline symmetry axis of the monitor (40° target) and the other target location was 20° to the left of midline (– 20° target; see Fig. 4). The distance from the bottom, center of the monitor was 18 cm. Participants responded after delays of 100 ms (7 trials) or 10,000 ms (84 trials). The 100 ms delay trials were control trials used to confirm that the touchscreen was responding accurately and participants could touch the screen accurately. These trials were

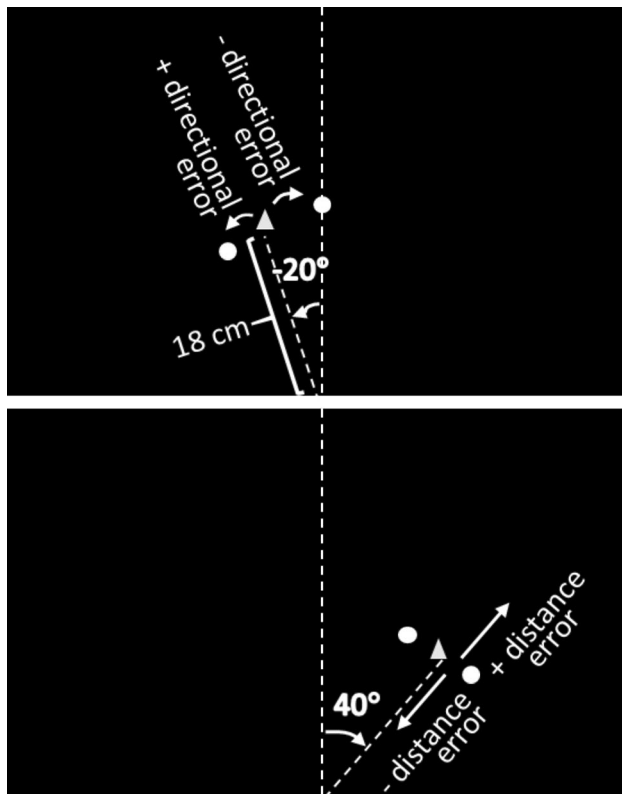


Fig. 4 Diagrams of the spatial working memory task showing the target locations (white triangles) for the **a** – 20° target and **b** 40° target. Gray dots mark approximate distractor locations for the 20° distractor for each target location

not included in any of the analyses. Six of the 10,000 ms delay trials to each target location did not have a distractor, and there were six trials to each target location for each distractor location (-20° , -12.5° , -5° , 5° , 12.5° , 20° from target location) for a total of 36 trials with a distractor to each target location. Distractors presented toward midline relative to the target location were coded as negative (-20° , -12.5° , -5°) while those presented outside of the target location relative to midline were coded as positive (5° , 12.5° , 20° ; see Fig. 4). Note that in visual angle the distractor locations ranged from approximately 1.25° – 5.20° from the target location. The distractor appeared 2500 ms prior to the go signal and remained illuminated for 1000 ms. See Fig. 5 for a schematic of a complete trial sequence. Trial order was randomized.

Method of analysis

The computer recorded up to two touches of the screen. Thus, if a participant inadvertently touched the screen prior to their intended response, they could make a second response. The computer calculated the absolute distance between each touch and the target location. The touch closest

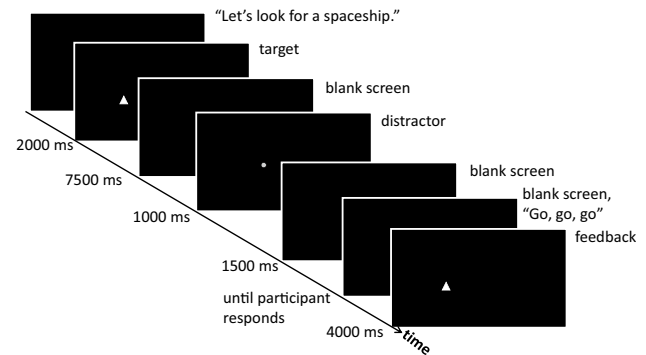


Fig. 5 Schematic of trial sequence with a distractor presented during the delay

to the target location was used in all analyses. Occasionally the touchscreen recorded both touches at the very top or bottom of the screen. These trials were removed from the data and not analyzed (82 total trials, 1.0% of trials). In addition, outliers more than 3 standard deviations from the mean absolute error were removed (94 trials, 1.2%). Constant directional errors and constant distance errors were computed for the remaining trials. Directional errors toward midline were coded as negative and errors away from midline were coded as positive. Distance errors that undershot the target were coded as negative and those that overshot the target were coded as positive (see Fig. 4). The computer also calculated reaction time as the time between the start of the “go” signal and the first touch of the screen.

Results

Constant directional errors, constant distance errors, and reaction times were examined in separate models using Proc Mixed in SAS. A compound symmetry covariance structure was used for all models. The models included the main effects for target (-20° , 40°), distractor (-20° , -12.5° , -5° , no distractor, 5° , 12.5° , 20°), and gender (male, female) and the interaction effects. Trial number was entered as a control. Restricted maximum likelihood (REML) was used in reporting model parameters, and degrees of freedom were calculated using the containment method.

Constant directional errors

In the model of constant directional error there was a significant main effect of target, $F(1, 101) = 48.63$, $p < 0.0001$, and a significant main effect of distractor, $F(6, 606) = 15.77$, $p < 0.0001$. There were no other significant main effects or interactions. Overall, responses were biased away from midline, but responses to the 40° target were less biased than the -20° target (40° target: $M = 1.23$, $SE = 0.16$; -20° target: $M = 1.86$, $SE = 0.16$).

To illustrate the influence of the distractor on constant directional error, we computed the difference between mean constant directional error on the no distractor trials and the distractor trials for each of the distractors (Fig. 6). Positive differences are biases away from the distractor and negative differences are biases toward the distractor. As can be seen in the figure, memory responses were generally biased away from distractors, with the bias largest for those close to the target location. To follow-up on the effect of distractor and test the hypotheses, planned t tests (two-tailed) were conducted comparing mean constant directional error for each distractor location to mean constant directional error for no distractor trials. Constant directional errors on trials with distractors -5° , 5° , 12.5° , and 20° from the target were significantly different from the no distractor trials (-5° distractor: $t(606)=3.60$, $p<0.001$; 5° distractor: $t(606)=3.81$, $p<0.001$; 12.5° distractor: $t(606)=3.90$, $p<0.001$; 20° distractor: $t(606)=2.16$, $p=0.032$). Constant directional errors on trials with distractors -20° and -12.5° from the target were not significantly different from the no distractor trials (-20° distractor: $t(606)=0.01$, $p=0.994$, -12.5° distractor: $t(600)=1.68$, $p=0.093$). Thus, the results partially supported the first hypothesis in that biases depended on the distance between the distractor and target location, but even the closest distractor location resulted in a bias away from the distractor. In support of the second hypothesis, all three of the distractors located outside of the target relative to midline significantly influenced memory responses, while only one distractor between midline and the target location influenced responses.

Constant distance errors

In the analysis of constant distance errors, the only significant effects were a main effect of target $F(1, 101)=11.12$,

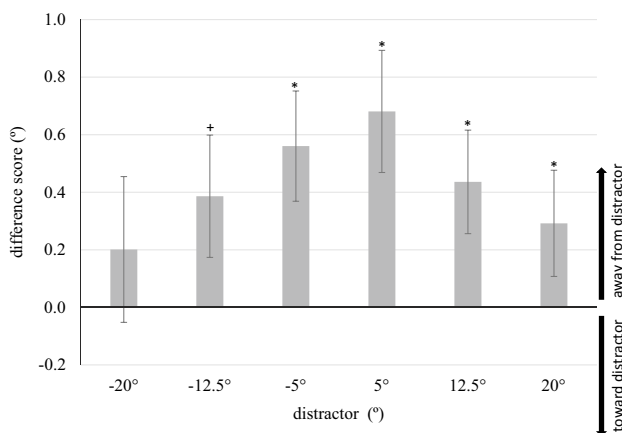


Fig. 6 Difference between mean constant directional error from trials without a distractor and mean constant directional error for trials with a distractor in Experiment 1. Errors represent the standard error of the mean. * $p<0.05$, + $p<0.10$

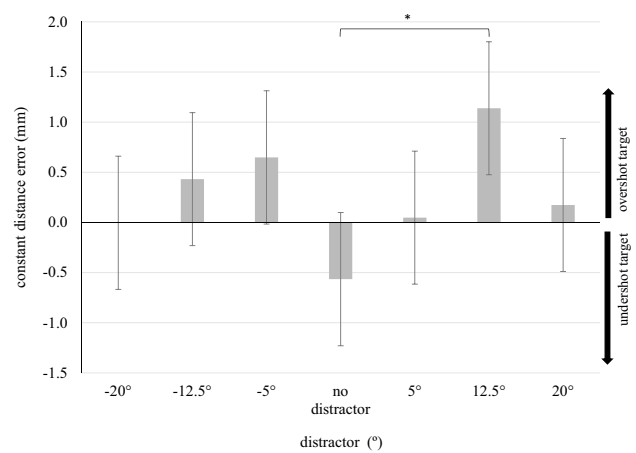


Fig. 7 Mean constant distance error in Experiment 1 for no distractor trials and each of the distractors. Errors represent the standard error of the mean. * $p<0.05$

$p=0.0001$, and a main effect of distractor, $F(6, 606)=2.38$, $p=0.028$. Responses to the 40° target overshoot the center of the target (40° target: $M=0.71$ mm, $SE=0.59$ mm), and responses to the -20° target slightly undershot the center of the target (-20° target: $M=-0.17$, $SE=0.59$). Overall, however, mean constant distance errors to each target were not significantly different from zero (40° target: $t(101)=1.19$, $p=0.235$, -20° target: $t(101)=-0.29$, $p=0.769$). Mean constant distance error for each distractor is shown in Fig. 7. As can be seen in the figure, when there was no distractor mean constant error was slightly below the center of the target (an undershoot), and when there was a distractor, mean constant errors were more above the center of the target, or slightly overshoot the target (an overshoot). To follow-up on the effect of distractor, t tests (two-tailed) were conducted comparing constant distance error for each distractor location to constant distance error for no distractor trials, using a Bonferroni adjusted p value of 0.008 for each test. Only constant distance errors on trials with the distractor at 12.5° were significantly different from the no distractor trials, $t(606)=-3.44$, $p<0.001$, all other p 's >0.01 .

Response time

To determine if the distractor location had a significant effect on reaction time, we analyzed reaction time, the time from the start of the "go" signal to first contact with the touch-screen. It is important to note that this is a measure of time to first touch, not time to initiate a response. There was a significant main effect of target, $F(1, 101)=8.15$, $p=0.005$, and a main effect of distractor, $F(6, 606)=2.39$, $p=0.027$. There were no other significant effects. On average, participants were faster to respond to the 40° target than the -20° target (40° target: $M=1528$ ms, $SE=40.6$ ms; -20°

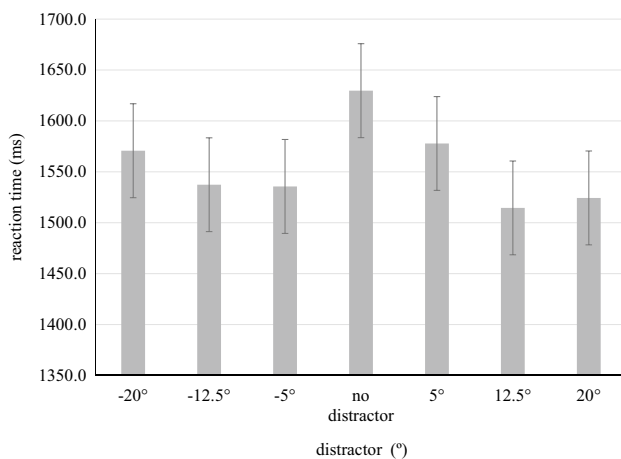


Fig. 8 Mean response time for no distractor trials and each of the distractors. Errors represent the standard error of the mean

target: $M = 1584$ ms, $SE = 40.6$ ms). This difference is to be expected given that majority of adults are right-handed and reaching to the -20° target involves crossing midline. Overall, responses following a distractor were slightly faster than the no distractor trials (Fig. 8), but there was no difference between the different distractors. The go signal was always a set time after the distractor onset, so the distractor may have acted as a cue for the go signal. To determine if this had any effect on the directional errors, we conducted the same analysis as above with reaction time added as a control. Although reaction time was significant, $F(1, 8173) = 10.60$, $p = 0.001$, the main effects of target, $F(1, 101) = 47.22$, $p < 0.0001$, and distractor, $F(6, 606) = 15.76$, $p < 0.0001$, remained significant, and showed the same pattern of error.

Discussion

Generally, spatial memory responses were biased away from distractors presented during the maintenance period of the spatial recall task. These biases away from distractors were similar to biases caused by reference axes (e.g., Spencer & Hund, 2002) and by nearby landmarks (Schmidt, Werner, & Diedrichsen, 2003); however, the distractors in this study were present only during the maintenance period of the task. This bias away from distractors contrasts with previous research that found that memory responses were not biased by distractors when participants could ignore them (Johnson & Spencer, 2016) or were biased toward sudden onsets when they were near the target location (Herwig, Beisert, & Schneider, 2010; Van der Stigchel et al., 2007). Although the repulsion effects in this study differed from previous research with adults, our findings replicated previous results with children (Schutte, Keiser, & Beattie, 2017), and indicate developmental continuity from childhood to adulthood. These results, however, differed from the pattern

predicated by the DFT model simulations. The simulations of the model predicted that memory responses would be either not biased or biased toward distractors near the target and away from distractors farther from the target. However, participants' responses were more strongly biased away from distractors near the target than by distractors far from the target. The difference between the model and the empirical results will be discussed further in the general discussion.

The difference between the biases in this study and those found in previous studies could be due to task differences. One possibility is that the closest distractor was still too far from the target location to generate a bias toward the distractor. The visual angle between the target locations and each distractor ranged from 1.2° to 5.2° , which ranged from closer to farther from the target when compared to other studies (Herwig, Beisert, & Schneider, 2010; Johnson & Spencer, 2016; Van der Stigchel et al., 2007). Thus, the explanation that the closest distractor was still too far from the target to generate a bias toward the distractor seems unlikely.

A second possibility, which was proposed by Schutte, Keiser, and Beattie (2017), is that the length of time the distractor was present allowed inhibitory processes to become active. The distractor in the current study was present for at least twice as long as previous studies with adults. Johnson and Spencer (2016) was the next longest at 500 ms. This difference in timing may be significant, because inhibition appears to be a slower process. Initially, a distractor may automatically attract attention (Schreij, Owens, & Theeuwes, 2008). Attention that is exogenously captured by a sudden onset can disengage from the onset after about 150 ms (Theeuwes, Atchley, & Kramer, 2000). If the distractor remains present for significantly longer than 150 ms, an inhibitory mechanism may engage that actively inhibits the distractor location and results in a bias away from the distractor. For example, in visual attention tasks inhibition of return emerges after about 300 ms (Samuel & Kat, 2003). Thus, a distractor that is present for a short period of time, e.g., 100–400 ms (Herwig et al., 2010; Van der Stigchel et al., 2007), may capture attention, but may not be present long enough for inhibitory mechanisms to engage. Experiment 2 varied the timing of the distractor presentation and the target presentation to determine whether memory biases vary as a result of the timing.

Experiment 2

The first goal of Experiment 2 was to determine if more closely matching the timing of the target, delay, and distractor to previous studies would result in a bias toward the distractor. To test this hypothesis, half of the trials had a delay of 1500 ms, and the timing of the distractor was shortened to 500 ms. We chose to shorten both the delay and

the distractor to maximize the likelihood of responses being biased toward the distractor while keeping the number of trials manageable. We hypothesized that these trials would result in a bias toward the distractor. The second goal was to replicate the results of Experiment 1, so we included trials with the same delay and distractor timing as in Experiment 1. On half of the trials the amount of time the target was illuminated was shortened to 500 ms. We hypothesized that this would result in a less stable memory, and, as a result, larger errors.

Methods

Participants

Fifty-nine college students (43 females, 16 males) participated in the study. Participants received course credit for their participation. The study was approved by the institutional review board and was performed in accordance with the ethical standards in the 1964 Declaration of Helsinki and its later amendments. All participants provided informed consent, and reported normal or corrected-to-normal vision. One additional participant was not included in the analyses due to experimenter error. As in Experiment 1, participants completed the Ohio State University traumatic brain injury (TBI) identification method interview (Corrigan & Bogner, 2007; Bogner & Corrigan, 2009). Eleven participants (6 females, 5 males) reported a TBI, and their data were excluded from these analyses.

Apparatus

The apparatus for Experiment 2 was the same as Experiment 1, except the monitor used for this study was a 36.9-inch \times 21.5-inch (93.7 cm \times 54.6 cm) liquid crystal display (LCD) touch screen computer monitor (Sharp, Inc.) with a resolution of 1920 \times 1200 pixels.

Procedure

The procedure was the same as in Experiment 1, except participants completed 96 test trials (48 trials to each target). Participants completed two trial types: short timing and long timing. In the short timing trials, the total length of the delay was 1500 ms. The distractor illuminated 500 ms after the target turned off and remained illuminated for 500 ms. The long timing trials replicated the trials in Experiment 1. For both trial types, we varied the timing of the target. On half of the trials it was illuminated for 1500 ms, the same as Experiment 1, and for the other half it was illuminated for 500 ms. To decrease the number of trials participants had to complete, we only used the two closest distractor locations, -5° and 5° from the target location.

Method of analysis

The method of analysis was the same as in Experiment 1 with a few differences. The touchscreen in this experiment did not record any touches at the very top or bottom of the screen. As in Experiment 1, outliers more than three standard deviations from the mean absolute error were removed (49 trials, 0.09%). Constant directional error and constant distance error were computed for the remaining trials.

Results

As in Experiment 1, constant directional errors, constant distance errors, and response times were examined in separate models using Proc Mixed in SAS. A compound symmetry covariance structure was used for all models. The models included the main effects for target (-20° , 40°), target timing, (500 ms, 1500 ms), and distractor (-5° , no distractor, 5°), and the interactions of target, target timing, and distractor. Trial number and gender (male, female) were entered as controls. Restricted maximum likelihood (REML) was used in reporting model parameters, and degrees of freedom were calculated using the Containment method.

Constant directional errors

In the model of constant directional error for the short timing trials there was a significant main effect of target, $F(1, 47) = 87.97$, $p < 0.0001$, and a significant main effect of distractor, $F(2, 94) = 12.52$, $p < 0.0001$. There were no other significant main effects or interactions. Overall, responses were biased away from midline, but responses to the 40° target were less biased than the -20° target (40° target: $M = 0.55^\circ$, $SE = 0.12^\circ$; -20° target: $M = 1.42^\circ$, $SE = 0.12^\circ$). This pattern replicates the pattern of error from Experiment 1 with a shorter delay. As in Experiment 1, we computed the difference between mean constant directional error on the no distractor trials and the distractor trials for each of the distractors (Fig. 9, dark gray bars). As can be seen in the figure, memory responses were significantly biased away from the 5° distractor, $t(94) = 3.19$, $p = 0.0019$, and not significantly biased by the -5° distractor, $t(94) = 1.74$, $p = 0.0855$.

In the model of constant directional error for the long timing trials, the only significant effects were a significant main effect of target, $F(1, 47) = 63.91$, $p < 0.0001$, and a significant main effect of distractor, $F(2, 94) = 4.84$, $p = 0.0100$. Responses to the 40° target were less biased than the -20° target (40° target: $M = 1.33^\circ$, $SE = 0.25^\circ$; -20° target: $M = 2.56^\circ$, $SE = 0.26^\circ$). This pattern also replicated the pattern of error from Experiment 1. The difference between mean constant directional error on the no distractor trials and the -5° and 5° distractor trials is shown in Fig. 9, light gray bars. As can be seen in the figure, memory responses were

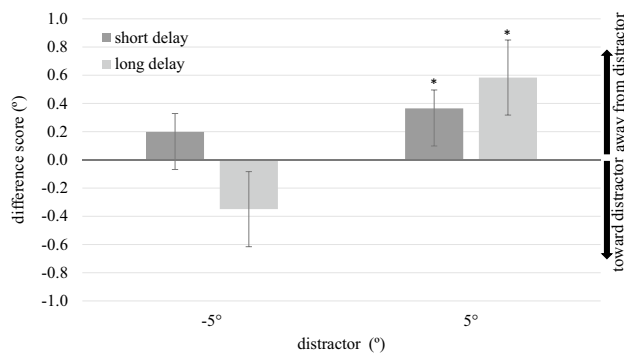


Fig. 9 Difference between mean constant directional error from trials without a distractor and mean constant directional error for trials with a distractor in Experiment 2. Errors represent the standard error of the mean. * $p < 0.05$

significantly biased away from the 5° distractor, $t(84) = 2.98$, $p = 0.0038$, but were not biased by the -5° distractor, $t(84) = -1.64$, $p = 0.1057$.

To compare bias on the two types of timing trials, we computed the mean difference between no delay trials and each distractor type for short timing trials and long timing trials. We then conducted paired t tests comparing mean differences across timing trials type for each distractor. There was a difference between timing trial types for both the -5° distractor, $t(47) = -2.25$, $p = 0.0291$, and the 5° distractor, $t(47) = -3.99$, $p = 0.0002$. For the -5° distractor trials, responses in the short timing trials were farther from the distractor than in the long timing trials, and the opposite was true for the 5° distractor trials. When the distractor was 5° from the target, responses in the long timing trials were farther from the distractor than in the short timing trials, although responses in both trial types were biased away from the distractor.

Constant distance errors

In the model of constant distance error for the short timing trials, there was a significant main effect of target, $F(1, 47) = 8.94$, $p = 0.0044$ and a significant main effect of target timing, $F(1, 47) = 5.97$, $p = 0.0184$. Participants undershot the center of the -20° target more than that 40° target (-20°: $M = -3.11$ mm, $SE = 0.53$ mm; 40°: $M = -3.95$ mm, $SE = 0.53$ mm). In addition, responses when the target was illuminated for 500 ms undershot the center of the target more than when the target was illuminated for 1500 ms (500 ms: $M = -3.88$ mm, $SE = 0.53$ mm; 1500 ms: $M = -3.19$ mm, $SE = 0.53$ mm).

In the model of constant distance error for the long timing trials there was only a significant main effect of target timing, $F(1, 47) = 4.37$, $p = 0.0421$. When the target was on for only 500 ms, participants undershot the center of the target

more than when the target was on for 1500 ms (500 ms: $M = -1.68$ mm, $SE = 1.01$ mm; 1500 ms: $M = -0.76$ mm, $SE = 1.01$ mm).

Response time

As in Experiment 1, we analyzed response time, the time from the start of the “go” signal to first contact with the touchscreen. In the short timing trials, there was a significant main effect of distractor, $F(2, 94) = 22.90$, $p < 0.0001$. There were no other significant effects. As in Experiment 1, responses following a distractor were slightly faster than the no distractor trials (-5° distractor vs. no distractor: $t(94) = -6.20$, $p < 0.0001$; no distractor vs. 5° distractor: $t(94) = 5.46$, $p < 0.0001$; -5° distractor: $M = 1836$ ms, $SE = 65$ ms; no distractor: $M = 1994$ ms, $SE = 65$ ms; 5° distractor: $M = 1854$ ms, $SE = 65$ ms), but there was no difference between the 5° and -5° distractors, $t(84) = -0.05$, $p = 0.9593$. We conducted the same constant directional error analysis as above with reaction time added as a control. Reaction time was not significant, and the results were the same as above.

In the analysis of response time for the long timing trials there were significant main effects of target, $F(1, 47) = 10.30$, $p = 0.0024$, and distractor, $F(2, 94) = 7.50$, $p = 0.0010$. On average, responses to the 40° target were faster than the -20° target (40° target: $M = 2001$ ms, $SE = 71$ ms; -20° target: $M = 2074$ ms, $SE = 71$ ms). Responses following the -5° distractor were significantly faster than the no distractor trials, $t(94) = -3.86$, $p = 0.0002$ (-5° distractor: $M = 1987$ ms, $SE = 72$ ms; no distractor: $M = 2095$ ms, $SE = 72$ ms). Responses following the 5° distractor were also faster than the no distractor trials, $t(94) = 2.22$, $p = 0.0289$ (5° distractor: $M = 2033$ ms, $SE = 72$ ms). There was no difference between the 5° and -5° distractors, $t(94) = -1.65$, $p = 0.1032$. Again, we conducted the same constant directional error analysis as above with reaction time added as a control. Reaction time was not significant, and the results were the same as above.

Discussion

Results of the long timing trials partially replicated Experiment 1. Specifically, as in Experiment 1, responses following the 5° distractor were biased away from the distractor, but, unlike Experiment 1, responses following the -5° distractor were not biased away from the distractor. The hypothesis that shortening the timing of the delay and distractor would result in a bias toward the distractor was not supported. Instead, on the short timing trials, responses following the 5° distractor were biased away from the distractor, and responses following the -5° distractor were not biased. The length of time the target was presented also did not affect bias in directional

errors. It did, however, affect bias for distance errors. Participants were more likely to undershoot the target location when the target was illuminated for only 500 ms, suggesting the location may not have been as accurately encoded.

Replicating results from Experiment 1, responses following a distractor were faster than when there was no distractor, but including response time in the models did not change the results of the constant directional error analysis. Thus, as in Experiment 1, differences in reaction time could not account for the biases related to the distractor.

This leaves open the question of why there are differences between these results and previous research. Although timing may influence the bias, i.e., a distractor that is 500 ms is still present longer than in some of the previous experiments, it seems unlikely that timing alone can account for the differences. Thus, future research should follow up on other differences to determine what factors, other than timing and distance from the target, influence whether or not distractors cause attraction or repulsion.

General discussion

Although results of both experiments found that memory responses were biased away from distractors, the pattern of bias found in the experiments differed from the pattern predicted by the DFT model of SWM. The first hypothesis generated from simulations of the model predicted that memory responses to the target location would be biased toward distractors near the target and away from distractors farther from the target. However, participants' responses in Experiment 1 were more strongly biased away from distractors near the target than by distractors farther from the target.

In the DFT model, distortions in SWM emerge as the result of the interactions between populations of neurons. Attraction emerges as the result of excitatory interactions, and repulsion emerges as the result of inhibition from a layer of inhibitory neurons. Thus, a peak in SWM can drift toward or away from an input, depending on the location and timing of the input. In the model, distractor input near the target location induces drift toward the distractor due to overlapping excitatory input, while distractor input farther from the target location results in drift away from the distractor, if the distractor is present long enough for sufficient inhibition from the inhibitory layer to be input into SWM. Thus, the dynamics of attraction and repulsion from an input depend on both the timing and the location of the distractor input. Given the dynamics of the model, there are two possible reasons for the differences between the predictions generated by the model and the results of the behavioral data.

The first possibility is that differences between the task used by Spencer and Hund (2002) and the task used here may account for the difference between the model and

empirical data. The parameters in the model were based on parameters used by Schutte and Spencer (2009) to model data from Spencer and Hund (2002). Although the two tasks were very similar, they differed in some potentially significant ways. For example, the task space used in Spencer and Hund, a table top, was larger than the monitor used in this study. Size of the task space can influence spatial memory biases (Huttenlocher, Hedges, Corrigan, & Crawford, 2004). In support of this suggestion, mean constant error in Spencer and Hund (2002) was slightly larger than mean constant error in the no distractor trials in this study. Smaller constant error on the no distractor trials may suggest that memory was more stable, which in the model would be captured by narrower, more precise lateral interaction. Narrower interaction would also lead to biases away at smaller distances due to less overlap between the target peak and the excitatory input from the distractor and more overlap with the inhibition from the distractor. A narrower inhibitory input from the inhibitory field would also lead to less bias away from distractors at farther locations.

A second possible explanation for the difference between the model and the empirical data is that the repulsion is due to a strategic top-down process that is not captured in the model. Top-down control processes can operate during the maintenance period. Kuo, Stokes, and Nobre (2012) found that top-down attentional control could modulate the content being maintained in visual working memory. In addition, various types of search tasks have found that adults inhibit distractor locations (Cave & Zimmerman, 1997), and Munneke, Van der Stigchel, and Theeuwes (2008) found that adults could use a top-down inhibitory mechanism to inhibit a cued distractor location. In this study, the top-down mechanism would need to be an inhibitory process that increases inhibition at the distractor location and results in repulsion from the distractor. Essentially, this process would be equivalent to intentional inhibition of the distractor, because participants expect the distractor not to be at the target location. The distractor in previous research may not have been presented long enough for this process to engage (Herwig et al., 2010; Van der Stigchel et al., 2007), and in Johnson and Spencer (2016) the sudden-onset was at the target location on a subset of trials. The possibility of the sudden-onset appearing at the target location may have resulted in participants not engaging a top-down inhibitory mechanism, because on a portion of the trials it would result in inhibiting the target location. In the model, this inhibition could be an input at the distractor location that is only input to the inhibitory field. To examine whether an overall sharpening of interactions in the model could account for the results, we conducted additional post hoc simulations where we scaled the width of interactions and the width of inputs until we matched the size of the constant directional errors on the no distractor trials in Experiment 1. The best match was with

a scalar of 0.8625 (40° target: $M=1.27^\circ$, $SE=0.08^\circ$, -20° target: $M=1.72^\circ$, $SE=0.08^\circ$). We then ran a full simulation to test whether or not the distractor biases would match Experiment 1. The pattern of biases more closely matched those of Experiment 1, in that the model was not significantly biased toward any of the distractors. However, there was still no significant bias away for the -5° , 5° , or 12.5° distractors. We narrowed the widths further to determine if it is possible for the SWM peak to be biased away from the closer distractors. When we scaled the interaction and input widths by 0.85, the peak in the SWM field was biased away from all but the -5° distractor. The model's errors on the no distractor trials were smaller, however, than in Experiment 1 (40° target: $M=1.04^\circ$, $SE=0.07^\circ$, -20° target: $M=1.58^\circ$, $SE=0.08^\circ$). This simulation suggests that the DFT model of SWM may be able to capture some biases away from distractors without adding a top-down inhibitory mechanism, but the results do not fit the entire pattern of errors. In addition, these simulations are post hoc and do not explain how or why the width of interaction would vary between studies. Taken together, these simulations suggest that a mechanism is missing from this DFT model. We return to this issue below.

The second hypothesis generated by the model was that the influence of the distractor on memory would vary depending on the direction of the distractor from the target. Although results of both experiments varied depending on which side of the target the distractor was located, the pattern did not match that predicted by the simulations. In both experiments, the distractors that were on the same side as midline had less of an effect on memory responses than those on the opposite side. In Experiment 1, when the distractor was on the opposite side of the target from midline, all three distractor locations (5° , 12.5° , and 20°) influenced memory responses, but when the distractor was toward midline only the closest distractor (-5°) significantly biased memory responses. In Experiment 2, only the distractor that was opposite of midline (5°) biased memory responses. If memory for the target location drifted away from the midline symmetry axis of the monitor during the delay then, by the time the distractor appeared, the location being maintained in memory was closer to the outer distractors than the inner distractors. In the experiment, being closer to the outer distractors resulted in stronger repulsion from the outer distractors instead of the bias toward the distractor.

The difference in results between Experiment 1 and 2 on the trials with the distractor at -5° was unexpected. The difference may be due to the smaller number of participants in Experiment 2, although this seems unlikely given that for the long delay trials the bias was in the opposite direction, although not significant. A second possibility is that differences between the experiments resulted in differences in the results. The touchscreen in Experiment 2 was larger than

in Experiment 1, which might have influenced the results. Constant directional errors on the long delay trials with no distractor were slightly larger in Experiment 2 ($M=2.26^\circ$, $SE=0.27^\circ$) than in Experiment 1 ($M=1.65^\circ$, $SE=0.19^\circ$) which may have been due to the size of the monitor. The difference is small, but by the time the distractor appeared, memory would have drifted farther from the -5° distractor in Experiment 2 than in Experiment 1, which may have reduced its effect. It is also possible that including the short delay trials influenced performance. Having short delay trials may have resulted in a more accurate long-term memory of the target locations, which would have resulted in a more stable memory. Constant directional errors on the no distractor trials with the long delay, however, were not smaller than in Experiment 1, which suggests that memory was not more stable.

In addition to differing from the model's predictions, the results also differed from previous research that found that the memory responses of adults were biased toward distractors (Herwig, Beisert, & Schneider, 2010; Johnson & Spencer, 2016; Van der Stigchel et al., 2007). These results, however, replicate the bias away from distractors found with children (Schutte, Keiser, & Beattie, 2017). As discussed previously, the difference in results does not appear to be due to a difference in timing or a difference in how close the distractor was to the target. Other differences between studies should be examined to see if they affect biases. For example, to avoid adding potential landmarks to the task space and to keep it as similar as possible to the study with children (Schutte et al. 2017), we did not use a fixation point. Researchers instructed participants to look toward the center of the screen and ignore the distractor, but we did not control whether or not they looked at the distractor. It is possible that looking at the distractor allows a more precise perception of its location relative to the target location, and this increased precision results in memory being biased away from the distractor. Future research should test this possibility.

The results of this study present challenges for the dynamic field theory of spatial working memory. In its current form, the model cannot capture the bias away from near distractors found in both Experiment 1 and 2. This pattern of error suggests that the model needs an additional executive component that can differentiate targets from distractors and inhibit the location of distractors. Toepper and colleagues (2010) found that activation in dorsolateral prefrontal cortex increased when distractors were presented during the encoding phase of a spatial span memory task. They interpreted this to mean that active suppression of distractors involves an executive inhibitory component. This executive inhibitory component is currently missing from the DFT model of spatial working memory.

Currently, the model differentiates targets and distractors based simply on whether or not there is already a peak in the SWM field. The model needs a process that would allow it to

encode the directions for the task, i.e., “remember the blue triangles,” and then process both the “what” and “where” dimensions of the stimuli, and use the “what” dimension to decide which locations are encoded and which are inhibited. Although these additional steps may sound relatively simple, the model would need several additional processes. First, the model would need a process that holds in memory the relevant dimension for differentiating targets from distractors (e.g., the color blue). Second, when a stimulus is presented the model would need to encode both ‘what’ and ‘where’ and be able to integrate the two. Previous DFT models have successfully done this encoding and integration (e.g., Schneegans, Spencer, & Schöner, 2016). Third, the model would need a mechanism that determines if a stimulus is a target or a distractor based on the dimension being held in memory (e.g., “blue”). This mechanism could be similar to that used for associating objects and labels in the DFT model of object learning (Samuelson & Faubel, 2016). Finally, the model would need to send excitation or inhibition to the spatial working memory field depending on whether a perceived stimulus is a target or distractor.

This expansion of the model of spatial working memory would clearly be significant and is beyond the scope of this paper. However, many of these mechanisms have been implemented in other DFT models (see Schöner et al., 2016, for examples), suggesting that a DFT model could potentially capture the results of the current study. The model would also need to be flexible enough to capture the differences in the effects of distractors across studies. Additionally, in some contexts, inhibiting distractors may be counter-productive. For example, in Johnson and Spencer (2016) the stimulus that appeared during the delay sometimes appeared at the target location, so inhibiting it may have resulted in larger memory errors. Future work should focus on developing a more complete model of SWM that can account for these effects while still accounting for other effects, such as the bias away from the midline symmetry axis and the changes in SWM over development.

In summary, results of this study suggest that when maintaining a location in SWM, the spatial details of the task matter. When distractors are close to a target location, they are more likely to influence memory. How distractors influence memory, however, appears to vary depending on the specifics of the task. In at least some situations, the spatial memory system appears to be able to inhibit distractors. This inhibition, however, comes at a cost when distractors are near the remembered location. Specifically, memory is biased away from the distractor. This can result in either a more accurate or a less accurate memory of the target location, depending on the location of the distractor relative to the target location and other perceptual cues in the task space, such as the midline symmetry axis. Overall, these

results suggest a memory system in which attention and inhibitory effects are emergent phenomena, and, as a result, the system can deal flexibly with disruptions.

Compliance with ethical standards

Research involving human participants All procedures performed in studies involving human participants were approved by and in accordance with the ethical standards of the institutional review board, and with the 1964 Helsinki Declaration and its later amendments.

Informed consent Informed written consent was obtained from all individual participants included in the study.

Conflict of interest The authors declare that they have no conflict of interest. The datasets analyzed for the current study are available from the corresponding author on reasonable request. The code for the simulations is also available upon request.

Appendix

The model used for these simulations was the same as the model used by Schutte and Spencer (2009) in Simulation Experiment 3 with the addition of a distractor input. This appendix presents the equations and parameters used for the model. For more details, see Schutte and Spencer (2009).

Activation in the perceptual layer (PF) is governed by the equation:

$$\begin{aligned} \tau \dot{u}(x, t) = & -u(x, t) + h_u + \int c_{uu}(x - x') \Lambda_{uu}(u(x', t)) dx' \\ & + S_{ref}(x, t) + S_{tar}(x, t) + S_{distractor}(x, t) \\ & - \int c_{uv}(x - x') \Lambda_{uv}(u(x', t)) dx' \\ & + q \int dx' g_{noise}(x - x') \xi(x', t), \end{aligned}$$

where the rate of change of the activation level for each neuron across the spatial dimension, x , as a function of time, t , is determined by the current activation level, $u(x, t)$, the resting level, h_u , self-excitatory projections, $\int c_{uu}(x - x') \Lambda_{uu}(u(x', t)) dx'$ inhibitory projections from the Inhibitory layer (Inhib), $\int c_{uv}(x - x') \Lambda_{uv}(u(x', t)) dx'$, reference input, $S_{ref}(x, t)$, target input, $S_{tar}(x, t)$, distractor input, $S_{distractor}(x, t)$, and spatially correlated noise, $q \int dx' g_{noise}(x - x') \xi(x', t)$. The reference, target, and distractor inputs are Gaussians (see Table 1 for the width and strength of each Gaussian). The excitatory and inhibitory projections are determined by the convolution of a Gaussian kernel with a sigmoidal threshold function. The Gaussian kernel is specified by:

Table 1 Parameter values for simulations

Layer	τ	h	Self-excitation	Excitatory projection(s)	Inhibitory projection(s)	Reference input	Target input	Distractor input
u (PF)	80	-7	$c_{uu} = 1.90$ $\sigma_{uu} = 3.0$		$c_{uv} = 1.207$ $\sigma_{uv} = 5.7$ $k_{uv} = 0.05$	$c_{ref} = 16.638$ $\sigma_{ref} = 0.8$	$c_{tar} = 45$ $\sigma_{tar} = 3$	$c_{dis} = 12$ $\sigma_{dis} = 3$
v (Inhib)	10	-12		$c_{vu} = 4.7$ $\sigma_{vu} = 5.0$ $c_{vw} = 2.2$ $\sigma_{vw} = 6.0$				
w (SWM)	80	-6.5	$c_{ww} = 3.296$ $\sigma_{ww} = 5$	$c_{wu} = 1.75$ $\sigma_{wu} = 3$	$c_{wv} = 0.757$ $\sigma_{wv} = 35$ $k_{wv} = 0.05$	Reference and target inputs scaled by $c_s = 0.2$		

$$c(x - x') = c \exp \left[-\frac{(x - x')^2}{2\sigma^2} \right] - k,$$

with strength, c , width, σ , and resting level, k . The level of activation required to enter into the interaction is determined by the following sigmoid function:

$$\Lambda(u) = \frac{1}{1 + \exp[-\beta u]},$$

where β is the slope of the sigmoid. The slope determines whether neurons close to threshold (i.e., 0) contribute to the activation dynamics with lower slope values permitting graded activation near threshold to influence performance, and higher slope values ensuring that only above-threshold activation contributes to the activation dynamics.

The inhibitory layer, *inhib*, is governed by a similar equation:

$$\begin{aligned} \tau \dot{v}(x, t) = & -v(x, t) + h_v + \int c_{vu}(x - x') \Lambda_{vu}(u(x', t)) dx' \\ & - \int c_{vw}(x - x') \Lambda_{vw}(w(x', t)) dx' \\ & + q \int dx' g_{noise}(x - x') \varepsilon(x', t), \end{aligned}$$

As in the equation for PF, $\dot{v}(x, t)$ is the rate of change of the activation level for each neuron across the spatial dimension x , as a function of time, t , $v(x, t)$ is the current activation in the field, and, h_v , sets the resting level of the field. *Inhib* (v) receives input from both PF(u), $\int c_{vu}(x - x') \Lambda_{vu}(u(x', t)) dx'$, and SWM(w), $\int c_{vw}(x - x') \Lambda_{vw}(w(x', t)) dx'$. These projections are defined by the convolution of a Gaussian kernel with a sigmoidal threshold function using the same equations as the interaction in PF(u). As in PF(u), the final input to the field is noise, $q \int dx' g_{noise}(x - x') \varepsilon(x', t)$.

The SWM layer (w) is governed by a similar equation:

$$\begin{aligned} \tau \dot{w}(x, t) = & -w(x, t) + h_w + \int c_{ww}(x - x') \Lambda_{ww}(w(x', t)) dx' \\ & - \int c_{wv}(x - x') \Lambda_{wv}(v(x', t)) dx' \\ & + \int c_{wu}(x - x') \Lambda_{wu}(u(x', t)) dx' \\ & + c_s S_{ref}(x, t) + c_s S_{tar}(x, t) + \\ & + q \int dx' g_{noise}(x - x') \varepsilon(x', t), \end{aligned}$$

As in the previous equations, $w(x, t)$ is the current activation in the field, and h_w is the resting level. Inputs to SWM include self-excitation, $\int c_{ww}(x - x') \Lambda_{ww}(w(x', t)) dx'$, lateral inhibition from *Inhib*, $\int c_{wv}(x - x') \Lambda_{wv}(v(x', t)) dx'$, and input from PF, $\int c_{wu}(x - x') \Lambda_{wu}(u(x', t)) dx'$. SWM also receives weak direct reference input, $S_{ref}(x, t)$, and target input, $S_{tar}(x, t)$, all scaled by c_s . The final input to the field is spatially correlated noise, $\int dx' g_{noise}(x - x') \varepsilon(x', t)$.

With the exception of the addition of a distractor input, parameter values were the same as in Schutte and Spencer (2009; see Table 1). The size of the fields was 397 units with 1.2 units equal to 1 degree, and noise strength was set to 0.135 with noise width, the spatial spread of noise, set to 1.

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