Reference-related inhibition produces enhanced position discrimination and fast repulsion near axes of symmetry

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Models proposed to account for reference frame effects in spatial cognition often account for performance in some tasks well, but fail to generalize to other tasks. Here, we demonstrate that a new process account of spatial working memory—the dynamic field theory (DFT)—can bridge the gap between perceptual and memory processes in position discrimination and spatial recall, highlighting that the processes underlying spatial recall also operate in position discrimination. In six experiments, we tested two novel predictions of the DFT: first, that discrimination is enhanced near symmetry axes, especially when the perceptual salience of the axis is increased; and second, that performance far from a reference axis depends on the direction in which the second stimulus is presented. The DFT also predicts the magnitude of this direction-dependent modulation. These effects arise from reference-related inhibition in the theory. We discuss how the processes captured by the DFT relate to existing psychophysical models and operate across a diverse array of spatial tasks.

The role of reference frames has been the focus of study across a number of research areas in spatial cognition. For instance, perception researchers have examined the frames of reference people use when perceiving locations, including the role of attention in the formation of object-centered reference frames (e.g., Vecera & Farah, 1994). Researchers in motor control have addressed related issues, examining how people transform extrinsic sensory information into the intrinsic reference frames needed to control the eyes, head, and arms (Andersen, 1995; Darling & Miller, 1993; Feigenbaum & Rolls, 1991; Graziano, Hu, & Gross, 1997; Soechting & Flanders, 1989). Finally, researchers in spatial memory have investigated how spatial information is maintained relative to reference frames during both short-term (Hund & Spencer, 2003; Huttenlocher, Hedges, & Duncan, 1991; Huttenlocher, Newcombe, & Sandberg, 1994; Spencer & Hund, 2002, 2003) and long-term (e.g., Hund & Plumert, 2005; McNamara & Diwadkar, 1997) delays.

Although this collection of research has led to a rich empirical understanding of which frames of reference people use in different situations, there has been less emphasis on the processes that give rise to reference frame effects (see Deneve & Pouget, 2003; Mozer & Sitton, 1998; and Pouget, Deneve, & Duhamel, 2002, for steps in this direction). Moreover, few accounts have been proposed to help understand how the processes that produce reference frame effects in one content area relate to reference-related processes in another content area. For instance, psychophysical models of position discrimination provide insight into why discrimination performance is better near a reference frame (see Johnson & Scobey, 1982; Kinchla, 1971; Leibowitz, 1955; Palmer, 1986a, 1986b). However, such accounts say little about why people show reference-related distortions in spatial memory (see, e.g., Huttenlocher et al., 1991; Spencer & Hund, 2002). Conversely, models of spatial memory provide accounts for why people show memory distortions (see Huttenlocher et al., 1991), but such accounts offer little insight into reference-related perceptual processes.

The goal of this study was to test a new process account of spatial working memory (SWM)—the dynamic field theory (DFT)—that has the potential to link reference effects across traditional research areas. This theory was initially proposed to explain spatial recall biases near frames of reference (see Schutte, Spencer, & Schöner, 2003; Spencer & Schöner, 2003, 2006). Here, we extend the theory to provide a neurally plausible account of the mechanisms underlying enhanced position discrimination

near frames of reference (see, e.g., Kinchla, 1971; Palmer, 1986a, 1986b). We then use this theory to generate two novel predictions about reference-related position discrimination performance. Results from six experiments support the predictions of the theory, providing an important first step toward a more task-general view of the processes that underlie reference frame effects in spatial cognition. In the sections that follow, we provide a brief overview of the DFT as it has been applied to memory biases in spatial recall tasks. Then, we extend the theory to account for performance in position discrimination tasks and generate two novel predictions.

The Dynamic Field Theory

The DFT is a new process-based theory of SWM instantiated in a neural network model that captures children's and adults' performance in spatial recall tasks (Schutte et al., 2003; Spencer & Schöner, 2003, 2006). In these tasks, participants are shown a target object, typically within a geometric figure such as a V-frame (see, e.g., Engebretson & Huttenlocher, 1996; Tversky & Schiano, 1989), and are asked to remember the target's location. When reproducing the target location after a short delay, adults show sys-

tematic biases away from the edges and symmetry axes of the frame (Engebretson & Huttenlocher, 1996; Spencer & Hund, 2002; Tversky & Schiano, 1989). For instance, adults in the V-frame task show biases away from the left and right edges of the frame as well as biases away from the frame's midline symmetry axis. These biases increase systematically across delays of 0–20 sec (Spencer & Hund, 2002; Werner & Diedrichsen, 2002).

Why are participants' responses generally biased away from reference frames in this task? According to the DFT, these biases are a by-product of coupling SWM processes to processes that perceive the edges and symmetry axes in the task space. Although this keeps remembered information anchored to the world during the delay despite changes in eye position, head position, and so on, excitatory and inhibitory traces left by locking onto a reference frame can distort memory, resulting in recall errors. This account is illustrated in Figure 1, which shows a simulation of the DFT during a single spatial recall trial. The model consists of five fields. The top panel in the figure represents the perceptual field, which captures the perception of the spatial context and the target presentation. The next two panels correspond to the excitatory (u) and in-
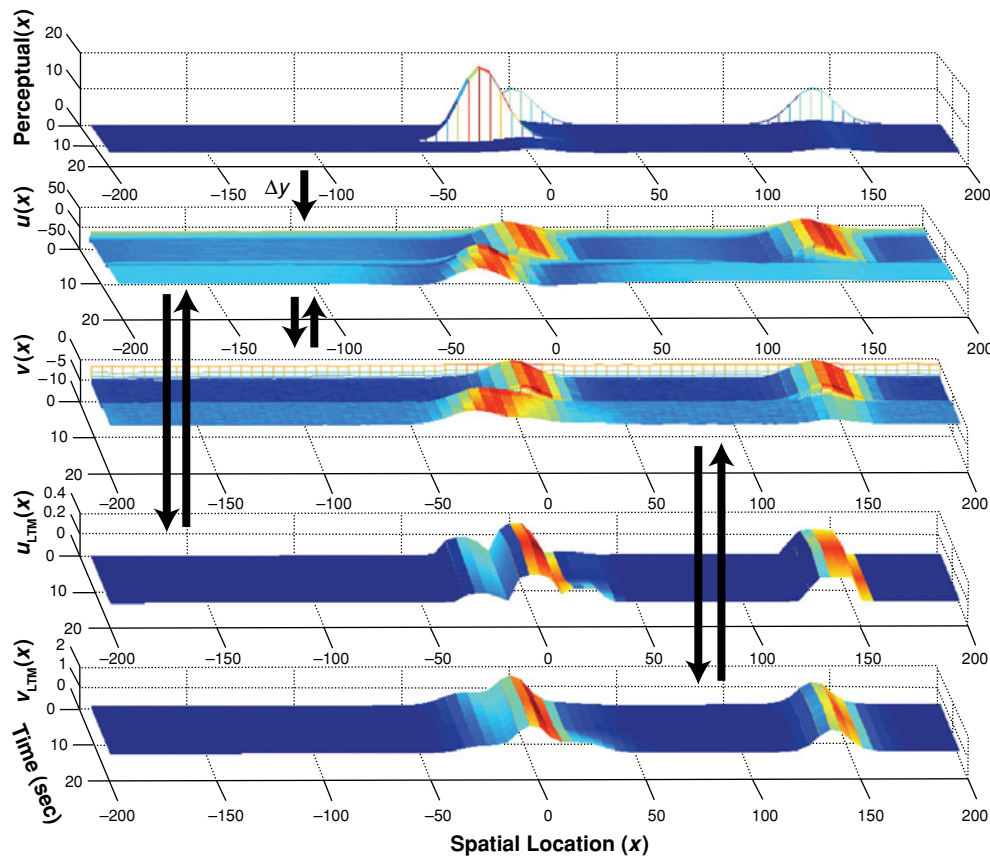

Figure 1. A simulation of the dynamic field model. From top to bottom, the panels represent perceptual field, excitatory spatial working memory (SWM) field, inhibitory SWM field, excitatory long-term memory (LTM) field, and inhibitory LTM field. Interaction between fields is represented by arrows. In each field, location is represented along the *x*-axis, activation along the *y*-axis, and time along the *z*-axis. The trial begins at the back of the figure and moves forward. See text for additional details.

hibitory (v) layers of SWM. These layers actively maintain spatial information during short-term delays via recurrent interactions. The bottom two panels in the figure show activation in the excitatory (u_{LTM}) and inhibitory (v_{LTM}) long-term memory layers. Activation in these fields is reciprocally coupled to activation in the respective working memory layers. In each panel, the x-axis consists of a collection of spatially tuned neurons with Location 0 aligned with the midline symmetry axis of the frame and Location 140 aligned with the right edge of the frame. The y-axis shows each neuron's activation level. Finally, time is captured along the z-axis, with the beginning of the trial at the back of each panel.

The simulation in Figure 1 begins with SWM in reference mode. In this mode, the u and v layers establish peaks of activation at locations associated with the perceived frames of reference in the perceptual field—in this case, Locations 0 (midline symmetry axis) and 140 (right edge of the frame). Note that, for the sake of simplicity, we did not include the left edge of the frame in the simulation. The simulation runs for 10 sec in this mode. Then, the target location is displayed in the task space at -20 (see large Gaussian input in the perceptual field at 10 sec). This event moves SWM into memory mode. In this mode, the field selects the dominant input—in this case, the target—and forms a self-sustaining peak at the corresponding location in memory. This activation peak is maintained during the memory delay (10–20 sec) via locally excitatory and laterally inhibitory interactions among the u and v layers. Importantly, although working memory maintains target-related information during the delay, the peak of activation in working memory drifts away from 0 (midline). This drift is caused by the strong inhibitory input around Location 0 from the inhibitory long-term memory (see the v_{LTM} field in Figure 1), built up when the model was in reference mode. Over the delay, as the inhibitory long-term memory feeds back into the inhibitory layer of working memory (v), laterally inhibitory processes receive an extra inhibitory boost around midline. Consequently, when the model responds at the end of the trial by selecting the location associated with the maximum activation in the u layer, it makes a leftward error. Thus, activation peaks are repelled away from reference frames—the same biases observed in many spatial recall tasks.

Position Discrimination in the DFT

The central goal of the present article was to extend the DFT beyond spatial recall to determine the generality of the reference-related processes captured by this account. To examine this issue, we asked whether or not the DFT can capture reference-related position discrimination effects. That is, can this theory explain why position discrimination is enhanced near reference frames (Kinchla, 1971; Palmer, 1986a, 1986b; Werner & Diedrichsen, 2002)? There are two key differences between the position discrimination task and the spatial recall task. First, in the former task, two stimuli are presented in quick succession. Second, participants must judge whether these stimuli are in the *same* position or *different* positions, rather than re-

produce the location as is usually required in recall tasks. The DFT is equipped to address the first difference between the two tasks because of the time-dependent nature of the theory—adding a second stimulus presentation and adjusting the stimulus presentation times is straightforward. Our approach to the second difference—to the use of *same/different* judgments—is illustrated in Figure 2.

Figure 2A shows a schematic of activation in the u layer of SWM generated by the presentation of two close stimuli, A and B. Because their points are near one another, locally excitatory interactions among neurons in this layer will cause the activation associated with these stimuli to blend and increase over time, ultimately combining to form a single peak of activation in SWM. Once this peak reaches a critical threshold—an activation level above 0—the model makes a *same* response. Figure 2B shows a simulation of the DFT during a *same* trial. As in Figure 1, this figure shows location along the x-axis, activation along the y-axis, and time along the z-axis. (Note that the trial begins at the front of this figure.) The first stimulus (S1) is presented after 100 time steps and begins building activation in the working memory field. At Time Step 500, S1 is removed, and the second stimulus (S2) is presented nearby. Because S1 and S2 are close together, activation left by the presentation of S1 blends with the new input generated by the presentation of S2. Over the next 400 time steps, activation builds to form a peak that pierces threshold. At the end of the trial (Time Step 900), the model responds *same*.

Figure 2C shows a schematic of how the model makes a *different* response. In this panel, Points A and B are far from each other. Consequently, the activation associated with these points does not overlap, and an activation peak fails to grow in the u layer. In this case, the response threshold is not pierced within the time window allowed for a response (2 sec), and the model responds *different*. Figure 2D shows a simulation of a *different* trial in the DFT. Again, S1 is presented at Time Step 100 and begins building activation in the working memory field. At Time Step 500, S1 is removed and S2 is presented far from S1. Now, the activation from S1 fails to blend with the activation from S2. By the end of the trial, therefore, activation does not pierce threshold and the model responds *different*.

The approach to position discrimination depicted in Figure 2 is similar in several ways to the approach of psychophysical models of discrimination. For instance, Kinchla (1971) proposed that the encoding of each stimulus can be represented as a probability distribution with a variance influenced by both *encoding noise* and *memory noise*. In his model, memory noise is a time-dependent source of variance that reflects increasing uncertainty over delay. *Same* and *different* responses are then computed on the basis of the overlap of these distributions relative to a response criterion. At face value, the probability distributions in Kinchla's model are similar to the activation profiles shown in Figure 2, and responses in both models are strongly influenced by the overlap of these distributions relative to a response criterion. Given these parallels, our model can be thought of as a neurally plausible implementation of Kinchla's ideas.
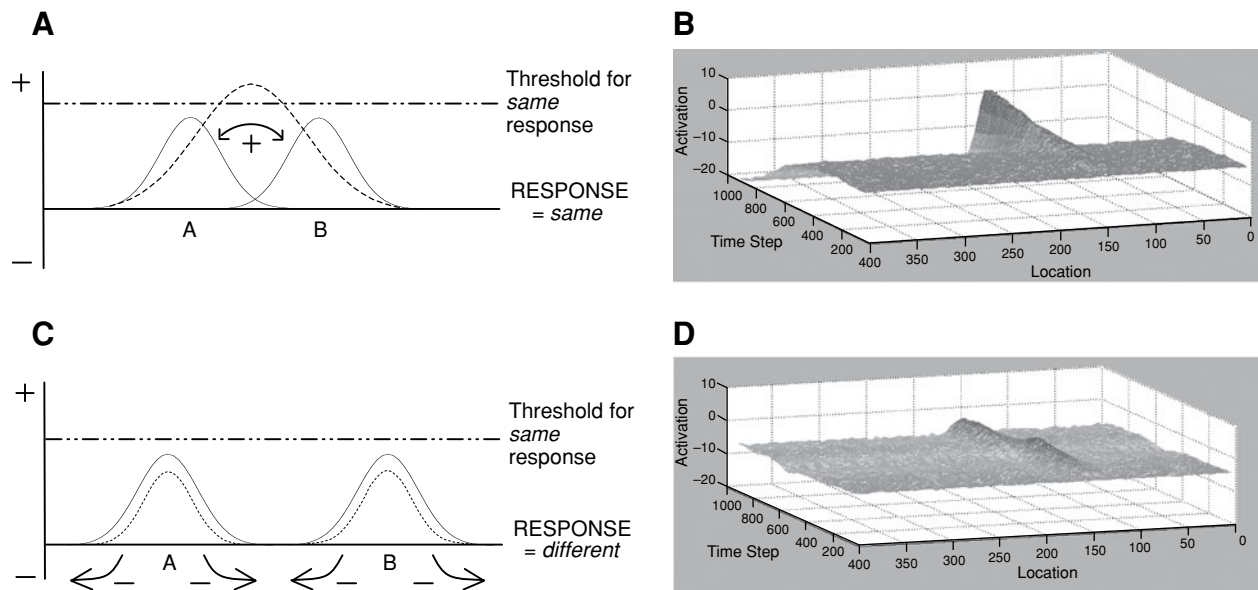
Figure 2. Position discrimination in the DFT. Two points, A and B, are presented near (panel A) or far from (panel C) each other. Solid curves represent initial activation associated with each location. Dashed curves show activation affected by local excitation and lateral inhibition. On the right are corresponding model simulations. When the stimuli are presented near each other, the activation profiles combine to form a single peak that pierces threshold (panel B). When the stimuli are presented far from each other, their activation profiles fail to overlap and, therefore, do not pierce threshold (panel D).

Nevertheless, there are important differences between the models. Most critically, the DFT specifies the neural mechanisms that underlie position discrimination. Rather than modeling the representation of stimuli using hypothetical probability distributions, the DFT represents the stimuli as patterns of activation in a neural network in which such patterns are emergent in real time from the network's activation dynamics. Importantly, multiple factors influence the real-time evolution of activation, including factors intrinsic to the network that are not included in Kinchla's (1971) model. For instance, a local excitation/lateral inhibition interaction function governs how neurons in the model interact with one another. The shape of this function has a major influence on whether or not inputs to the model will blend over time. This influence is above and beyond the encoding precision captured by the spatial characteristics of the inputs. The interaction function also contributes to the variance of the model's output. Specifically, the interaction function influences the stability of activation patterns through time, which affects the variability of the network's behavior from trial to trial. Again, this contribution is above and beyond, for instance, the noise level in the model, highlighting that the DFT makes contributions to variance that are not included in Kinchla's model. Kinchla, in contrast, distinguished two sources of variance—encoding and memory noise—that are not included in our model. Rather, we used a single white noise process in all our simulations.

Finally, in what sense is our model neurally plausible? First, our model is based on established neural principles (e.g., locally excitatory/laterally inhibitory interactions among neurons). These close ties stem from initial work

modeling visual cortical dynamics (Amari, 1977). Our model is also related to recent neural network approaches to working memory that capture the biophysical details of cortical dynamics (e.g., the details of neurotransmitter action; see Compte, Brunel, Goldman-Rakic, & Wang, 2000). Second, previous work has shown that dynamic fields can be directly estimated using population coding techniques in both visual cortex (Jancke et al., 1999) and motor cortex (Bastian, Riehle, Erlhagen, & Schöner, 1998; Bastian, Schöner, & Riehle, 2003; see Erlhagen, Bastian, Jancke, Riehle, & Schöner, 1999, for methodological details). Thus, although the tests of our model reported here are strictly behavioral in nature, there are principled ties to neurophysiology that lay the groundwork for future explorations of brain–behavior relations.

Capturing Enhanced Position Discrimination Near Reference Frames

Given our approach to generating *same/different* judgments in the DFT, can we use this account to explain why position discrimination is enhanced near reference frames (see Kinchla, 1971; Palmer, 1986a, 1986b; Werner & Diedrichsen, 2002)? Recall that reference-related spatial memory biases in the DFT are caused by spatial drift away from an inhibitory long-term memory input (see v_{LTM} in Figure 1) associated with the perceived reference frame. Given that the reference frame also leaves an excitatory long-term memory trace (see u_{LTM} in Figure 1), why do inhibitory effects dominate to the left and right of the axis? This occurs because inhibitory long-term memory traces are broader than excitatory traces in the model (a critical requirement for effective laterally inhibitory interactions

among neurons). Consequently, when inhibitory and excitatory long-term inputs sum, inhibitory effects dominate. This is illustrated in Figure 3A, which shows the sum of a broad inhibitory Gaussian reflecting the reference-related v_{LTM} from Figure 1 and a narrower excitatory Gaussian reflecting the reference-related u_{LTM} from Figure 1. As can be seen in the figure, inhibition dominates near the axis, although excitation plays a critical role as well—excitatory input around midline (i.e., Location 200) contributes to participants' low bias and low variability when targets are aligned with the axis (see, e.g., Spencer & Hund, 2002).

What are the consequences of strong inhibitory input to the left and right of midline? Because inhibition is relatively strong near the axis, activation associated with stimulus inputs in this region will be constrained by inhibition, leading to narrower activation peaks. Far from the axis, on the other hand, inhibition is weaker, so activation associated with stimulus inputs will spread more broadly. Because *same* responses in the model result from the overlap in activation produced by the presentation of S1 and S2 (see Figure 2), narrower peaks near the axis will lead to *different* responses at smaller separations—that is, to enhanced position discrimination near the axis.

Figure 3B shows simulations of the model showing this effect. In particular, we ran 50 simulations of the model shown in Figure 2 when S1 was presented at each of six target locations (T1–T6) corresponding to points 5º–30º to the right of midline (at 10-unit increments), with S2 presented at each of eight stimulus separations (0–7) to the right of S1 (at 3-unit increments). For each simulation, we recorded whether the model made a *same* or a *different* response— that is, whether or not the model showed above-threshold activation at the end of each trial. We then calculated the percent *same* responses across the 50 simulations at each target location and stimulus separation. Figure 3B shows the percent *same* responses across stimulus separations when S1 was presented at each target location. For targets near the reference, *same* responses began to decline at small stimulus separations (i.e., the model began to respond *different*), whereas the model responded *same* at larger separations for targets far from the reference. This is clearly seen at the horizontal line marking 75% *different* (i.e., 25% *same*)—the criterion typically used to indicate reliable discrimination performance. The model's performance for targets near the axis intersects with this line at smaller separations than does performance for targets far from the axis.
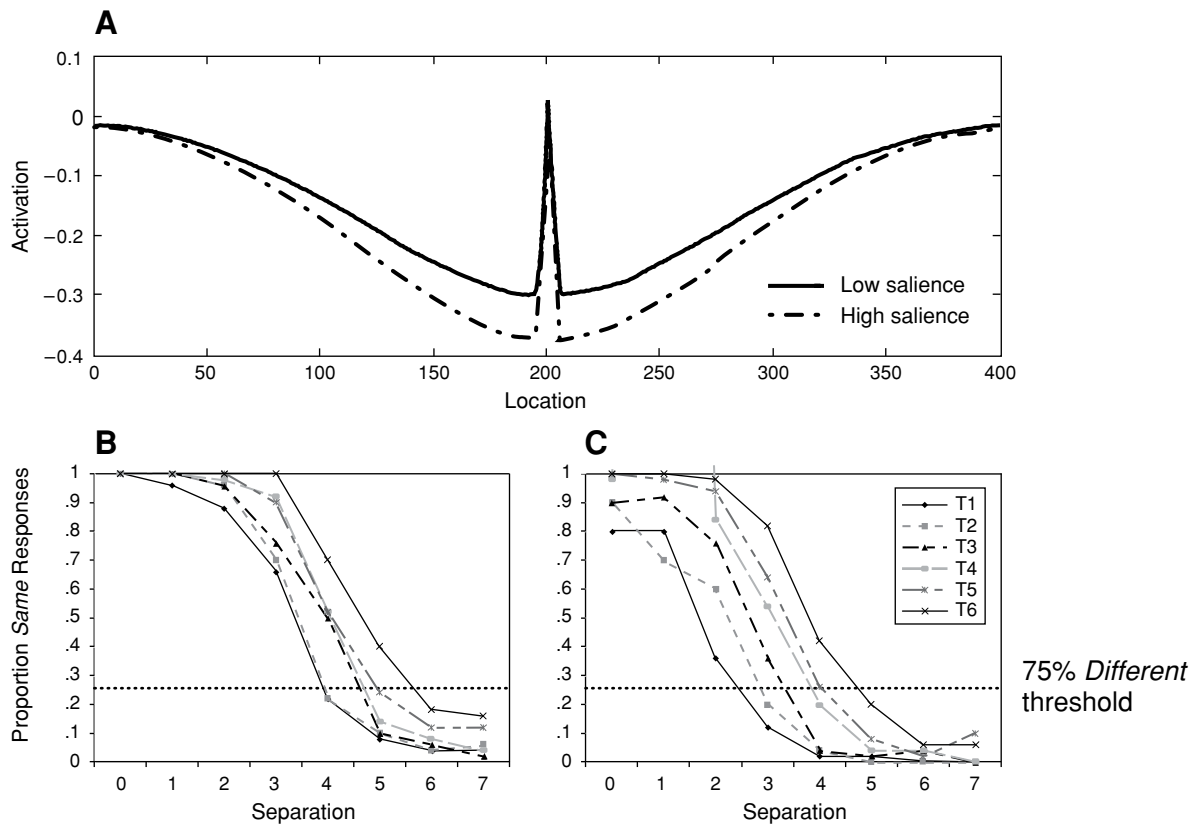

Figure 3. (A) Long-term memory input associated with low-salience (solid line) and high-salience (hatched line) reference input. Peaks near the reference are narrower due to stronger inhibition. DFT simulations show better performance near the axis than far from the axis with both low-salience (B) and high-salience (C) levels. Simulation results in panel C show that increasing salience improves discrimination performance. Each line represents the proportion of *same* responses (across 50 simulations) to one target location at different stimulus separations. Discrimination thresholds correspond to the separation at which the model responded *different* on 75% of trials. See text for additional details.

Like our approach to position discrimination, the DFT account of enhanced position discrimination near reference frames bears some similarity to Kinchla's (1971) account. In particular, Kinchla proposed that both encoding and memory noise are proportional to the separation between the stimulus and the reference frame, a type of Weber assumption. Although this is similar to the narrower activation profiles in the DFT, it is important to note that the DFT provides neurally plausible accounts of both the mechanism underlying enhanced discrimination (i.e., sharpened activation profiles are due to reference-related inhibition) and the origin of the reference effect (i.e., inhibition results from activation traces generated when the model locks onto perceived reference frames during the reference mode). In addition, Kinchla's model requires the explicit computation of the separation between a stimulus and the reference frame. This is not the case in the DFT, in which reference effects emerge due to metric interactions between the activation profiles produced by the stimuli and reference-related input.

Importantly, the same mechanism in the DFT that predicts enhanced discrimination near a reference also predicts that increasing the salience of the reference will further improve discrimination performance near the axis. Increasing the salience of the reference should lead to stronger inhibition near the axis, as is shown by the hatched line in Figure 3A. Stronger inhibition should produce further narrowing of peaks in the region near the axis, with a gradual reduction in this effect as targets are moved away from the axis. Figure 3C shows simulations of the DFT demonstrating this effect. Performance to targets near the reference (T1–T3) was better than performance in the low-salience simulations, with reliable *different* responding at smaller separations. Thus, reference-related inhibition improves performance near the reference, especially with higher salience.

Novel Predictions of the DFT

The mechanism that underlies enhanced discrimination near reference axes in the DFT leads to two novel predictions tested in the present study. First, according to the theory, the strength of reference-related inhibition should depend on the strength of the reference input. In particular, a more salient reference axis should generate more reference-related inhibition, which should, in turn, lead to more precise position discrimination. In Experiments 1–3, we tested this prediction by examining participants' position discrimination performance near the midline symmetry axis probed in our spatial memory research (see Spencer & Hund, 2002). We made this axis more salient by marking it. For instance, in one condition we displayed two dots along the axis but outside of the target presentation space. This manipulation was selected on the basis of a recent report that perception of symmetry is enhanced when dots are added to the symmetry axis of an object (Li & Westheimer, 1997). We also examined the generality of the enhancement effects by translating the symmetry axis off the midline of the table into an empty region of the task space—that is, into a region devoid of symmetry axes. The question here was whether or not we could create a salient

virtual axis in otherwise "empty" space (see also Werner & Diedrichsen, 2002).

The second prediction of the DFT is derived from a second consequence of reference-related inhibition: Such inhibition causes delay-dependent spatial drift. Recall that peaks of activation in the model are repelled away from reference axes during memory delays. Figure 4A shows how such effects arise from the same reference-related inhibition that leads to enhanced position discrimination near reference axes. For activation peaks near the reference, inhibition is roughly equal on both sides of the peak. This leads to narrower peaks, as described above, but does not create a bias for peaks to drift in either direction. Activation peaks farther away from the reference, however, rest on top of a stronger inhibitory gradient—that is, inhibition is greater on the side of the peak closer to the reference. In this case, activation will tend to grow in the direction of less inhibition—away from the reference. Note that the reference-related inhibitory profile shown in Figure 4A captures the complex pattern of repulsion effects in spatial recall tasks with accurate performance for targets aligned with the reference axis (where excitatory long-term memory input dominates). With this pattern, repulsion starts near 10°, becomes maximal near 20°, and decreases as it approaches 60° (Spencer & Hund, 2002).

To date, the timescale of these repulsion effects has been primarily examined empirically at relatively long delays (e.g., 5 sec or more; Spencer & Hund, 2002). If repulsion occurs quickly, however, then it should influence position discrimination as well, even though the delay is typically much shorter than those in spatial recall tasks. Recent data from Werner and Diedrichsen (2002) suggest that repulsion does occur at delays as short as 50 msec and, furthermore, that such *fast repulsion* produces an asymmetry in discrimination responses based on the direction of S2 relative to S1 (see Werner & Schmidt, 2000). Figures 4B and 4C show a schematic of such effects. If the activation peak associated with S1 is repelled away from the reference axis (see Figure 4B), it should overlap more with stimuli presented in the same direction—that is, away from the reference frame. Thus, when S2 is presented farther away from the reference frame than S1, participants should be more likely to respond *same*. Conversely, if S2 is presented in the opposite direction, participants should be more likely to respond *different*, even at relatively small stimulus separations (see Figure 4C). Importantly, such asymmetries should be maximal when the inhibitory gradient is large—that is, when S2 is far from the reference axis—and minimal when the gradient is small—that is, when S2 is near the reference axis. We tested these predictions in Experiments 4–6 by varying both the relative direction of the two stimuli as well as the proximity of the stimuli to a reference axis.

EXPERIMENT 1

The goal of this experiment was to test the first prediction of the DFT: that more salient reference axes should produce stronger reference-related enhancement of position discrimination. Participants viewed two dots pre-
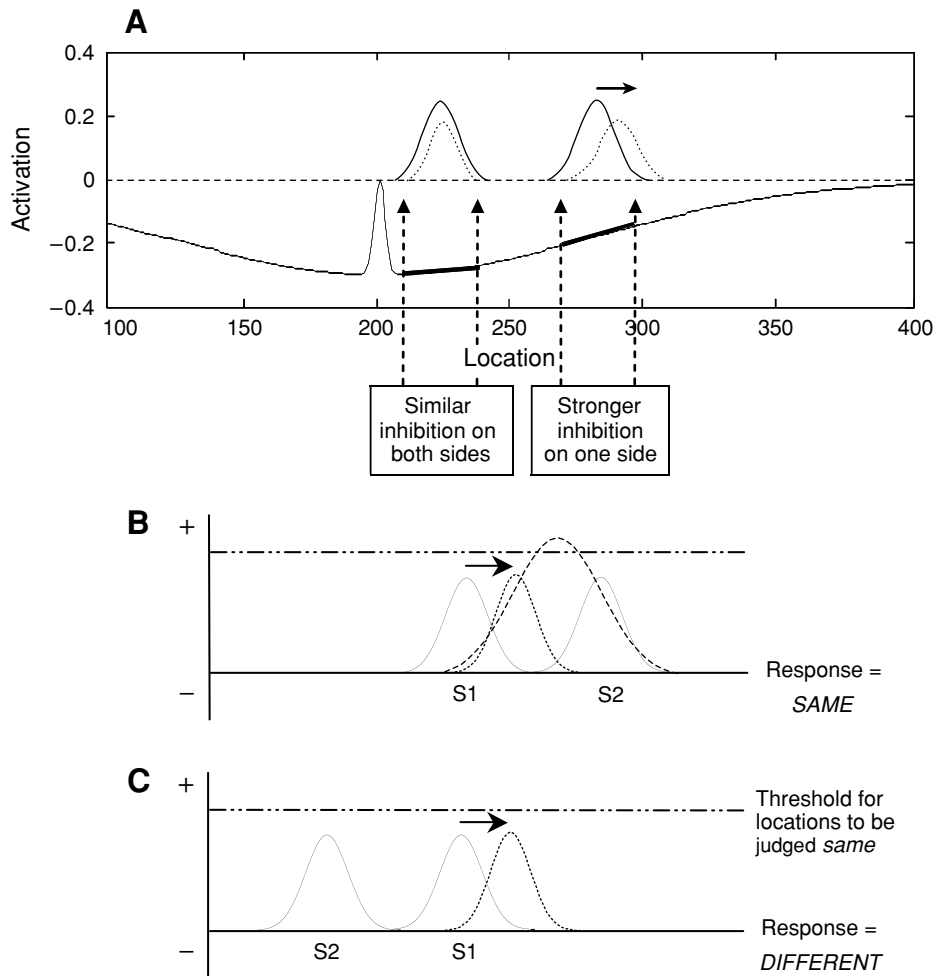
Figure 4. Illustration of how long-term memory input creates repulsion effects in the DFT (A). Solid curves represent initial activation associated with each stimulus. Dotted curves show activation at response initiation. Solid lines highlight the inhibitory gradient on either side of each activation peak. Panels B and C show how fast repulsion affects discrimination performance relative to the direction in which S2 is presented. When S2 is presented away from the axis (B), the S1 peak is repelled toward S2, leading to more overlap and a *same* response. When S2 is presented toward the axis (C), the S1 peak is repelled away from S2, leading to less overlap and a *different* response.

sented in succession on a tabletop and then identified if the dots were in the same location or in different locations. On each trial, stimuli were presented relatively near or far from the midline symmetry axis used in our previous spatial memory work (e.g., Spencer & Hund, 2002), with varying separations between the stimuli. The DFT predicts that discrimination will be better near midline than far from it—that is, that participants will be able to identify the two dots as *different* at smaller stimulus separations when they are presented near the midline of the table. In addition, discrimination near midline will be further improved with a more salient symmetry axis.

Method

Participants. The participants were 60 adults (38 females and 22 males, mean age = 22.4 years, *SD* = 7.5) with normal or corrected-to-normal vision. For their participation, the participants were either paid \$7/h or given research exposure credit in an introductory psychology course. Each participant completed two sessions on different days. Data from 5 additional participants were excluded: Three participants completed only one of the two sessions, and 2 participants did not meet the inclusion criterion (see below).

Apparatus. The participants were seated on a chair placed within an arc cut out from the side of a large (0.921 × 1.194 m) table. The surface of the table was homogeneous, and three edges of the table were covered with a curved border to occlude the corners from the participants' view. This eliminated the table's diagonal symmetry axes. Sessions were conducted in a dimly lit room with black curtains covering the walls and ceiling to limit the participants' use of external reference cues. Stimuli were projected onto the surface of the table (a rear projection surface) from below using a Barco 708 data projector. Throughout the procedure, the tabletop appeared black to the participants (0.0 cd/m^2 background luminance). Two types of images were used: yellow reference dots and white target dots. The luminance of the yellow dots was 0.742 cd/m^2, and the color index on the CIE 1932 system was $x = 0.321$, $y = 0.57$. The

white target dots had a luminance of 0.1462 cd/m^2, and the color index on the CIE 1932 system was $x = 0.266$, $y = 0.156$. While viewing stimuli, the participants placed their heads in a chinrest to ensure consistent viewing angle throughout the sessions (for details, see Table 1). A numeric keypad was attached to the base of the chinrest, out of the field of vision. The participants used the "1" and "3" keys on this keypad to indicate their *same* and *different* responses; because the keypad was not visible, these two keys were marked with Velcro, so they were identifiable by touch.

Procedure. After completing consent forms, the participants were seated at the table and positioned at the chinrest. A demonstration trial was shown to explain the trials. Demonstration trials were repeated as necessary until the participant understood the task, and most of the participants needed only one or two demonstrations. Once the participants understood the task, the practice trials began.

Each trial began with a 100-msec warning tone. In reference conditions, yellow dots marking the midline of the table appeared at the same time (see Experimental Design, below); in each trial, these dots remained visible until the participant entered a response. The warning tone was followed by a 1-sec delay and then a 500-msec presentation of the first stimulus dot (S1, 2 pixels in diameter). Next came a 500-msec delay (consisting of a 200-msec delay, a 100-msec warning tone, and a 200-msec delay), followed by a 500-msec presentation of the second stimulus dot (S2, 2 pixels in diameter). The 500-msec delay between S1 and S2 is similar to the delay used in other discrimination studies (e.g., Kinchla, 1971; Werner & Diedrichsen, 2002). Palmer (1986a) reported that at this delay participants do not perceive motion of the dots, but rather rely on perception of position. Once S2 disappeared, the participants had 2 sec to indicate if S1 and S2 were in the same location or in different locations by pressing the corresponding keys on the keypad. The keys that signaled *same* and *different* were counterbalanced across participants. If a participant did not respond within the allotted 2 sec, a penalty tone sounded. Once the response was entered, the next trial began. Note that the warning tones before S1 and S2 were used to indicate to the participants when the stimuli would appear. They were included to keep the procedure consistent with tasks in which variable delay lengths between S1 and S2 are used.

Each session began with 48 practice trials, followed by a short break in which the participants could ask questions. Then, test trials were presented in nine blocks of 48 trials, with optional breaks between blocks. All the participants took a mandatory break after Block 5 to prevent fatigue. In general, the participants took two to three breaks, totaling less than 5 min. Across the nine blocks, the participants completed a total of 432 test trials per session, presented in random order. Thus, there was a total of 864 test trials across the two sessions.

Experimental design. The participants were randomly assigned to one of three perceptual conditions (see Figures 5A–5C): no reference (NoRef), two-dot reference (2DotRef), and dotted line reference (DotLineRef). In the NoRef condition, the midline symmetry axis of the table was not explicitly marked. In the 2DotRef condition,

Table 1
Viewing Distance (in Centimeters), Elevation Angle, and Visual Angle to Stimuli in Experiment 1

Target	Viewing Distance	Elevation Angle	Visual Angle
5°	58.03	42.18°	1.29°
10°	57.96	42.10°	2.57°
15°	57.84	41.98°	3.83°
20°	57.68	41.79°	5.07°
25°	57.47	41.56°	6.26°
30°	57.21	41.27°	7.41°

Note—Viewing distance is the distance from the eye to the stimulus. Elevation angle is the vertical angle from the eye down to the tabletop. Visual angle is the angle from midline to the stimulus. All measurements are calculated to the first stimulus presented (S1).

two yellow dots were aligned with midline (see Figure 5B). The first dot (14 pixels in diameter) was centered at the bottom of the stimulus presentation area, 24 cm from the front edge of the table; the second dot (2 pixels in diameter) was centered at the top of the stimulus presentation area, 30 cm beyond the first dot. In the DotLineRef condition, the two dots were in the same locations as in the 2DotRef condition, but they were both the same size (2 pixels). In addition, yellow dots were added toward the front and back edges of the table, spaced 5.5 cm apart toward the front edge of the table and 10 cm apart toward the back edge (see Figure 5C).

In all conditions, six target locations were used for S1: 5°, 10°, 15°, 20°, 25°, and 30°, clockwise from the midline of the table. Targets were 15 cm from the position of the lower dot in the 2DotRef condition (see Figure 5). The visual angle and viewing distance from the participant to each target are given in Table 1. S2 was presented at eight horizontal distances, or stimulus separations, from S1: at 0, 1, 2, 3, 4, 5, 6, and 7 pixels. S2 was always to the right of S1 and away from the axis. A 1-pixel separation between S1 and S2 was equal to approximately 0.12° of visual angle. Each target–stimulus separation combination was presented once during each block of practice trials (total of 48 trials) and 18 times across the 18 blocks of test trials (total of 864 trials).

Method of analysis. To determine the stimulus separation necessary for the participants to discriminate the positions as different, we computed a discrimination threshold for each participant at each target location. In particular, for each participant we calculated the percentage of *same* responses for each target–stimulus separation combination. As an example, Figure 6A shows 1 participant's *same* responses across stimulus separations for each target. This pattern of responses was generally consistent across individuals. Figure 6B shows the DFT simulations of this condition for comparison. To ensure that the participants were attending throughout the sessions and following instructions, we adopted the inclusion criterion that all participants had to respond above 60% *same* for at least one stimulus separation per target. Two participants' responses failed to meet this criterion. Once each participant's percent *same* responses were tallied, we fit a probit function through the data for each target location across stimulus separations. The point on each curve that intersected with the 75% *different* (i.e., 25% *same*) line was used as the threshold, in pixels, for that target location for that participant.

Results

Figure 7 shows mean discrimination thresholds across targets and conditions. Thresholds were lowest at 5° and increased as targets were moved away from midline. In addition, thresholds were consistently lowest in the DotLineRef condition, higher in 2DotRef, and highest in the NoRef condition. To analyze these effects, we conducted a two-way ANOVA with target (5°, 10°, 15°, 20°, 25°, and 30°) as a within-subjects factor and condition (NoRef, 2DotRef, and DotLineRef) as a between-subjects factor. This analysis revealed a significant main effect of target [$F(5,53) = 15.17$, $p < .001$] and a significant target × condition interaction [$F(10,108) = 1.97$, $p < .05$]. Tests of simple effects revealed significant target effects in each condition [NoRef, $F(5,95) = 12.40$, $p < .001$; 2DotRef, $F(5,95) = 28.66$, $p < .001$; DotLineRef, $F(5,95) = 13.70$, $p < .001$]. Each of these effects was driven by lower discrimination thresholds at 5°, which increased systematically as they approached 30° (see Figure 7). Additional tests of simple effects revealed a marginally significant condition effect for the 25° target [$F(5,73) = 2.28$, $p = .055$] and a significant condition effect for the 30° target [$F(5,73) = 2.34$, $p < .05$]. As is shown in Figure 7, these condition

Midline Axis   Lateral Axis

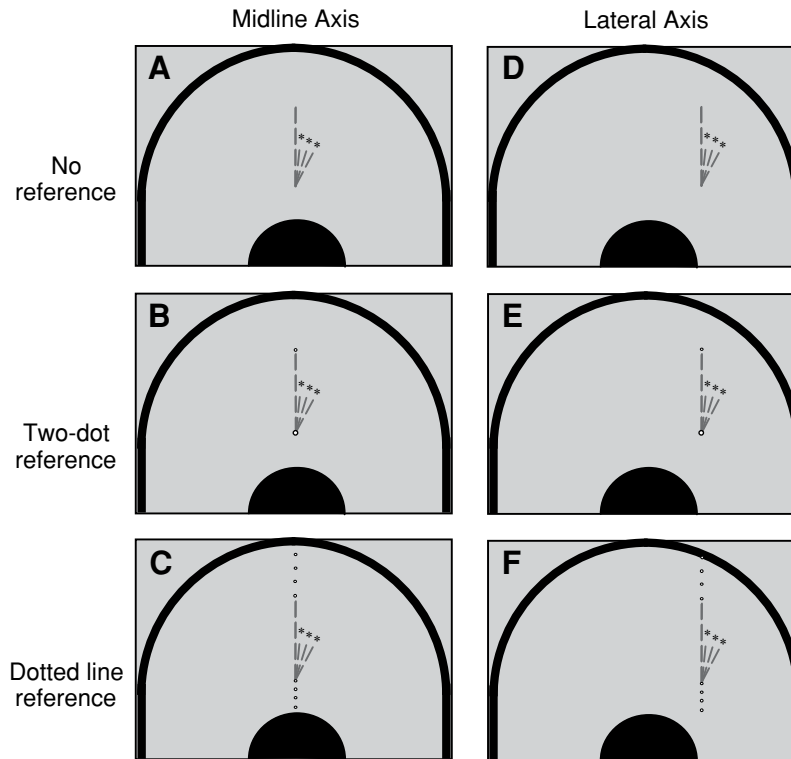**Figure 5. The six reference axis combinations used in all the experiments, presented in context with three possible targets (5º, 15º, and 25º). No reference (A), two-dot reference (B), and dotted-line reference (C) around the midline axis were used in Experiments 1, 3, and 4; in Experiments 5 and 6, only the two-dot reference (B) was used. (D–F) The same perceptual conditions around a lateral axis were used in Experiments 2–4. Dashed lines represent the axes of symmetry relative to which targets were positioned. This axis was not visible in the experiments.**

effects were driven by lower discrimination thresholds in the DotLineRef condition.

Discussion

The goal of this experiment was to test the DFT's prediction that a more salient reference axis will produce a greater enhancement of position discrimination near the axis than would a less salient axis. In all three conditions, there was a significant improvement in discrimination thresholds (i.e., lower thresholds) as the targets were presented closer to midline. This enhancement effect is consistent with previous studies that have reported enhanced discrimination near a reference dot (see Kinchla, 1971; Palmer, 1986a, 1986b). However, these results are the first to demonstrate that such effects generalize to symmetry axes. This provides an important link between our spatial memory research and the present report, because in our previous work we probed memory for locations near axes of symmetry (see Hund & Spencer, 2003; Spencer & Hund, 2002, 2003). In addition to the enhancement effect in all three conditions, we found that position discrimination was most precise in the condition with the most salient symmetry axis: the DotLineRef condition. These results support the first prediction of the DFT.

EXPERIMENT 2

In the present experiment, we examined whether or not the enhanced position discrimination effects evident in Experiment 1 generalize to other types of *virtual* axes. Werner and Schmidt (2000) demonstrated that spatial recall responses are biased away from a virtual axis formed by two dots positioned diagonally in the task space. This suggests that the reference effects examined in Experiment 1 are quite flexible. Thus, in the present experiment, we translated the perceptual cues from the 2DotRef and DotLineRef conditions 15 cm to the right of the midline axis. If enhanced discrimination is caused by processes linked to visual axes, as the DFT suggests, the results of the present experiment should replicate those of Experiment 1 around this lateral axis. Furthermore, because the lateral axis is not supported by perceptual structure in the NoRef condition, we should see no modulation of position discrimination across targets in this condition. This would suggest that we can effectively create and destroy reference axis effects in the empty region of space to the right of midline. (For related studies in which response biases were created in otherwise empty space, see, e.g., Sadalla, Burroughs, & Staplin, 1980.)
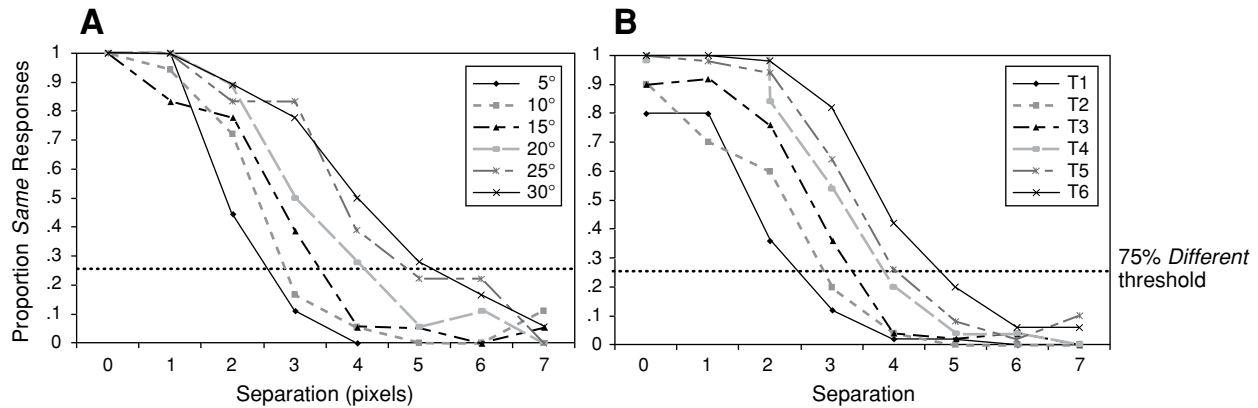
A

B

Figure 6. (A) Sample individual data from a participant in the 2DotRef condition in Experiment 1. Each line represents one target location. Points along these lines represent the proportion of the 18 trials at each stimulus separation on which the participant responded *same*. Discrimination thresholds correspond to the pixel separation at which the participant responded *different* reliably (i.e., on 75% of trials). This threshold was determined by fitting probit functions through the data for each target separately. Corresponding simulations of the DFT are shown in panel B.

Method

Participants. The participants were 60 adults (43 females and 17 males, mean age = 20.0 years, SD = 2.9) with normal or corrected-to-normal vision. Data from 6 additional participants were excluded for the following reasons: One participant completed only one of the two sessions, and 5 participants did not meet the inclusion criterion (see Experiment 1). All other participant details were identical to those of Experiment 1.

Apparatus and Procedure. In all details, the apparatus and procedure were identical to those of Experiment 1.

Experimental design. The experimental design was identical to that of Experiment 1 with one exception: In the present experiment, the stimulus display was translated 15 cm to the right of midline (see Figures 5D–5F). Thus, the reference axis was parallel to midline, and the stimulus dots appeared to the right of this lateral axis. Note

that this experiment also included a NoRef condition in which the axis was not marked, but the stimuli were still positioned relative to an imaginary axis 15 cm to the right of midline (see Figure 5D).

Method of analysis. The method of analysis was identical to that used in Experiment 1.

Results

Figure 8 shows mean discrimination thresholds across targets and conditions. Discrimination thresholds were once again lower at 5° than at 30° in each of the conditions; however, the modulation across targets in the NoRef condition was less pronounced than that in the other conditions. In addition, thresholds were consistently lowest in the 2DotRef condition, rather than in the DotLineRef
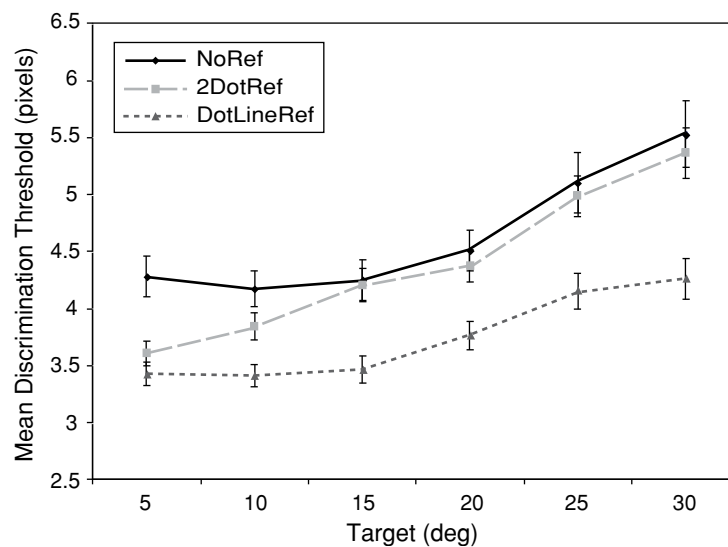

Figure 7. Mean discrimination thresholds across targets and conditions for Experiment 1. Discrimination thresholds indicate the pixel separation at which the participant reliably responded *different* on 75% of trials. Error bars represent one standard error.
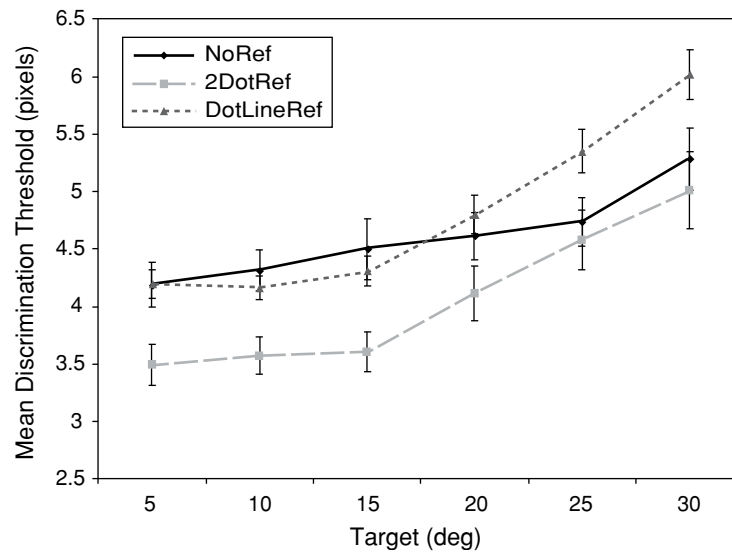
Figure 8. Mean discrimination thresholds across targets and conditions for Experiment 2. Error bars represent one standard error.

condition as in Experiment 1. To analyze these effects, we conducted a two-way ANOVA with the six targets (5°–30°) as a within-subjects factor and condition (NoRef vs. 2DotRef vs. DotLineRef) as a between-subjects factor. This analysis revealed a significant main effect of target [$F(5,53) = 9.85$, $p < .001$]. As can be seen in Figure 8, position discrimination was enhanced near the lateral reference axis, particularly when perceptual cues marked the axis. Nevertheless, the target $\times$ condition interaction did not reach significance. Although this contrasts with the results of Experiment 1, a preplanned one-way ANOVA indicated that, as was predicted, there was not a significant effect of target in the NoRef condition. This suggests that perceptual structure is a critical contributor to the enhancement effect reported here. Note that the slight modulation of thresholds across targets in the NoRef condition might reflect a far-reaching influence of the midline symmetry axis.

Discussion

The goal of this experiment was to determine whether or not the reference-related effects reported in Experiment 1 generalize to a second virtual axis to the right of midline. The results were mixed. On one hand, several of our predictions were confirmed: Discrimination performance was enhanced near the lateral reference axis, and there was not a significant modulation of discrimination across targets in the NoRef condition. On the other hand, we did not find the predicted interaction between target location and the salience of the reference axis. Indeed, thresholds for the conditions with added perceptual structure reversed order between Experiment 1 and Experiment 2. Specifically, DotLineRef had the lowest thresholds in Experiment 1, whereas 2DotRef showed the lowest thresholds in Experiment 2. It is possible that this reflects a real difference in the salience of our displays

when these are viewed around different axes. An alternative interpretation was suggested by further examination of the data. Variability was considerably higher in Experiment 2 than in Experiment 1: Average standard error was nearly 0.1 pixels higher in Experiment 2. Thus, it is possible that high between-subjects variability masked some effects in the present experiment. Given this possibility, we combined the factors from Experiments 1 and 2 into a single within-subjects design in the next experiment.

EXPERIMENT 3

Method

Participants. The participants were 10 adults (5 females and 5 males, mean age $= 23.3$ years, $SD = 2.5$) with normal or corrected-to-normal vision. The participants were paid \$15/h for their participation and completed 12 sessions, each on a different day.

Apparatus. In all details, the apparatus was identical to that used in Experiment 1.

Procedure. All procedural details were identical to those of Experiment 1, with the following exceptions. Instead of completing 2 sessions each, the participants in the present experiment completed 12 sessions each (2 sessions per condition–axis combination). As in Experiment 1, the 1st session consisted of 48 practice trials followed by 432 test trials. For all additional sessions, the number of practice trials was reduced to 24, but the number of test trials remained the same. Thus, across the 12 sessions, each participant completed 5,184 test trials.

Experimental design. In the previous experiments, the six target locations and eight stimulus separations used in Experiments 1 and 2 were probed in the same three perceptual conditions around both the midline (Experiment 1) and lateral (Experiment 2) axes. Unlike in the previous experiments, however, in Experiment 3 each of these factors varied within subjects. Thus, the participants completed 18 trials to each target–stimulus separation combination for each of the six condition–axis combinations (see Figure 5). All trials within a session were presented with one condition–axis combination; the order of the 12 sessions was randomized across subjects.

Method of analysis. The method of analysis was identical to that used in Experiment 1.
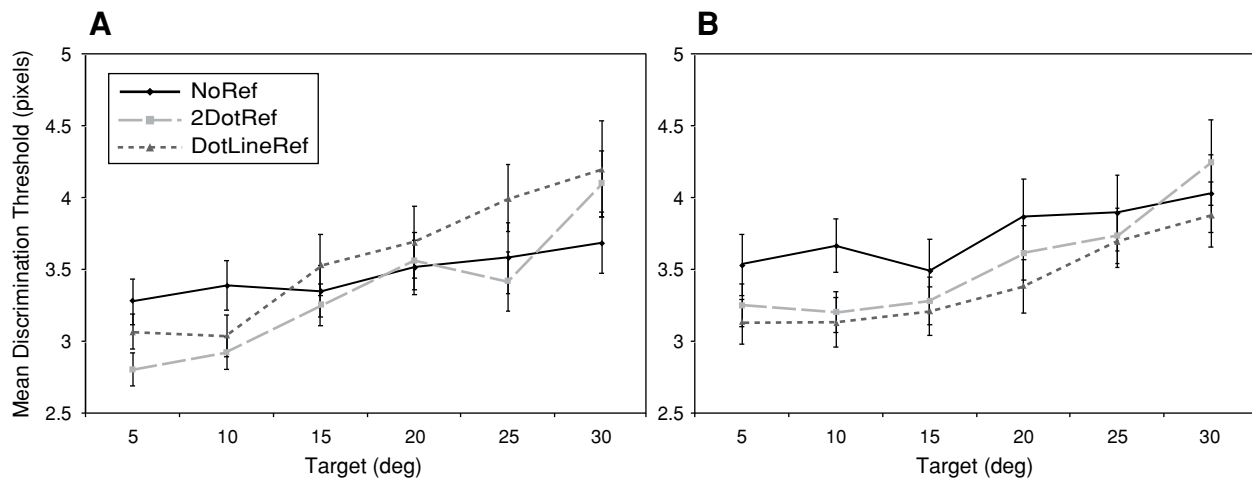
Figure 9. Mean discrimination thresholds across targets and conditions for the midline (A) and lateral (B) axes in Experiment 3. Error bars represent one standard error.

Results

Figure 9 shows mean discrimination thresholds across targets and conditions for the midline and lateral axes. As this figure shows, discrimination thresholds were more similar across conditions than in previous experiments. However, thresholds were still lower near the axis (5º) than far from the axis (30º). In addition, the NoRef condition showed the least modulation across targets.

Discrimination thresholds were compared in a three-way ANOVA with the six targets (5º–30º), condition (NoRef vs. 2DotRef vs. DotLineRef), and axis (midline vs. lateral) as within-subjects factors. This analysis revealed a significant main effect of target [$F(4,45) = 6.97$, $p < .001$] as well as a significant target × condition interaction [$F(10,90) = 3.74$, $p < .001$]. Tests of simple effects revealed a significant effect of condition for the 10º target [$F(2,18) = 4.56$, $p < .05$]. As Figure 9 shows, this effect was driven by higher discrimination thresholds in the NoRef condition than in the 2DotRef and DotLineRef conditions. This was confirmed by Tukey's HSD tests ($p < .05$), which showed significant differences between NoRef and 2DotRef and between NoRef and DotLineRef, but no difference between 2DotRef and DotLineRef. Additional tests of simple effects showed significant target main effects for the 2DotRef [$F(5,45) = 3.16$, $p < .001$] and DotLineRef [$F(5,45) = 11.09$, $p < .001$] conditions. By contrast, the effect of target in the NoRef condition was marginal [$F(5,45) = 2.15$, $p = .076$]. A preplanned ANOVA conducted to examine performance in the NoRef condition around the lateral axis revealed no significant modulation across targets [$F(5,5) = 1.92$, $p = .25$].

Discussion

In the present experiment, a within-subjects design was used to explore the robustness of the modulation of discrimination thresholds across targets, perceptual conditions, and reference axes. As in the first two experiments, position discrimination was enhanced near both the mid-line and a lateral axis. Moreover, results were consistent with the prediction of the DFT: Discrimination thresholds were significantly lower near salient reference frames. In particular, thresholds were lower in the 2DotRef and DotLineRef conditions than in the NoRef conditions, although the 2DotRef and DotLineRef displays proved to be of comparable salience. Additional analyses revealed that there was not a significant modulation of performance across targets in the NoRef condition around the lateral axis, suggesting that added perceptual structure was needed to create a reference frame in this otherwise empty region of the task space (for related results, see Werner & Schmidt, 2000). Considered together, then, the results of Experiments 1–3 demonstrate that position discrimination is enhanced near symmetry axes and, furthermore, that such effects are modulated by the salience of the reference axis, as predicted by the DFT.

EXPERIMENT 4

The primary goal of the present experiment was to test the second prediction of the DFT: that there should be an asymmetry in position discrimination responses based on the direction of S2 relative to S1, and that the magnitude of such effects should vary systematically with the distance of targets from a reference axis. Recall that activation peaks in the model are repelled from reference frames during short-term delays. If such repulsion occurs quickly, as data from Werner and Schmidt (2000) suggest, then position discrimination should be more accurate when S2 is presented toward the reference axis than when it is presented away from it (see Figure 4). Importantly, this asymmetry should be maximal when repulsion is large and minimal when repulsion is small. Maximal repulsion occurs in our recall task when targets are presented roughly 20º from midline (Spencer & Hund, 2002), with smaller repulsion closer to and farther from this axis. Thus, in the present experiment, we presented

targets near and far from the reference axes used in Experiment 3; however, we always presented S2 to the left of S1—that is, toward the reference axis. We predicted that this manipulation would produce lower discrimination thresholds to targets far from the reference axes (e.g., 25º) and comparable thresholds to targets near the axes (e.g., 5º) relative to performance in Experiment 3. In pursuit of a secondary goal—to determine whether or not more salient perceptual cues might lead to reliably lower thresholds—we increased the salience of our dotted line display. Recall that in Experiment 3, we found that the 2DotRef and DotLineRef conditions yielded comparable thresholds.

Method

Participants. The participants were 10 adults (9 females and 1 male, mean age = 19.7 years, SD = 1.1) with normal or corrected-to-normal vision. The participants were paid $10/h for their participation and completed six sessions, each on a different day. Data from 10 additional participants were excluded for the following reasons: Four participants did not complete all six sessions due to scheduling conflicts and/or lack of interest, 5 participants did not meet pretest requirements (see below), and 1 did not meet the inclusion criterion (see Experiment 1). (Note that although in the present experiment we excluded a relatively large proportion of participants for failing to meet pretest requirements, we relaxed this criterion in Experiments 5 and 6 and replicated the central results reported here. Thus, we do not think the pretest criterion substantially influenced our findings.)

Apparatus. In all details, the apparatus was identical to that used in Experiment 1.

Procedure. All procedural details were identical to those of Experiment 3, with one exception: Rather than completing two sessions for each condition–axis combination, only one session was needed for each condition–axis combination because we reduced the number of targets to three (see Experimental Design, below).

Experimental design. Three of the six target locations from Experiment 1 were used here: 5º, 15º, and 25º. The same eight stimulus separations were used as well, but in the present experiment S2 was always presented to the left of S1, and toward the axis rather than to the right as in the previous experiments. In addition, the DotLineRef

condition was replaced with a LineRef condition, in which the yellow dotted lines were replaced with green solid lines (retaining the gap in the stimulus presentation area).

Method of analysis. The method of analysis was identical to that used in Experiment 1, with one exception: The participants completed a pretest during the first session to assess whether or not the stimulus and target separations we used yielded differences in discrimination responses. In Experiments 1–3, there was a small number of participants who were very precise position discriminators. For example, 1 participant in Experiment 3 had an average discrimination threshold of 2.0 pixels (the overall average was 3.5 pixels). For these participants, the fixed range of stimuli we used was not appropriate. Although such individual differences limit the generalizability of the method of constant stimuli used in this study, this method is appropriate for testing the DFT because it allows us to compare discrimination performance to the same targets in the same task space used in our spatial recall studies.

The details of the pretest were as follows. Each participant completed the 2DotRef condition around the midline axis as the first session. Discrimination thresholds were computed for this session before any further sessions were scheduled. If the differences among the discrimination thresholds for all three targets were less than 0.5 pixels, the participant was excluded from further sessions and data for this participant were not included in analyses. Importantly, we did not evaluate which of the three targets' thresholds was highest; rather, we considered only the absolute differences.

Results

Figure 10 shows mean discrimination thresholds across targets and conditions separately for the midline and lateral axes. This figure shows that, unlike in the previous experiments, discrimination thresholds did not increase as the targets moved farther from the reference axes. Rather, thresholds decreased slightly across targets in all conditions. Importantly, thresholds close to the reference axes in the high-salience conditions (2DotRef, LineRef) were comparable to those in Experiment 3 (see Figure 9), whereas thresholds to targets far from the axes were lower than those in Experiment 3. Unlike in the previous experiments, however, thresholds in the NoRef conditions were quite high.
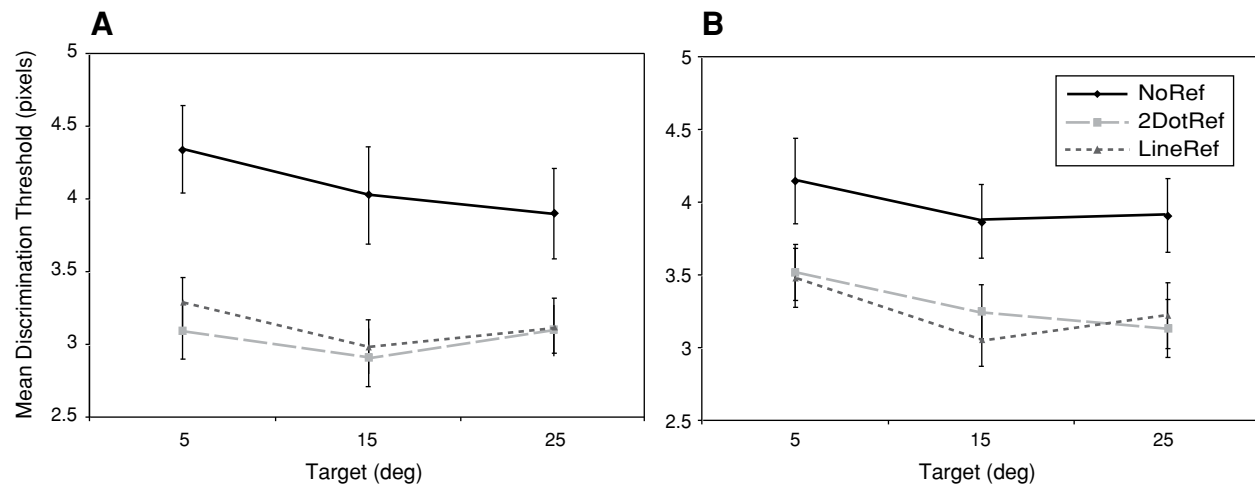

Figure 10. Mean discrimination thresholds across targets and conditions at the midline (A) and lateral (B) axes in Experiment 4. Error bars represent one standard error.

Discrimination thresholds were analyzed in a three-way ANOVA with target (5º vs. 15º vs. 25º), condition (NoRef vs. 2DotRef vs. LineRef), and axis (midline vs. lateral) as within-subjects factors. This analysis revealed a significant main effect of condition [$F(2,18) = 5.43$, $p < .05$]. Follow-up Tukey's HSD tests ($p < .05$) showed that the NoRef condition ($M = 4.03$) was significantly different from both the 2DotRef ($M = 3.17$) and the LineRef ($M = 3.19$) conditions, which did not differ significantly from each other. No other effects in the overall ANOVA reached significance; however, there was a trend toward a main effect of target [$F(2,18) = 2.65$, $p = .098$]. Unlike in the first three experiments, this target effect was due to *higher* discrimination thresholds for the close target ($M = 3.65$) than the far target ($M = 3.40$).

Discussion

The primary goal of this experiment was to test whether or not discrimination thresholds were lower to targets far from the reference axes and comparable to targets close to the axes relative to performance in Experiment 3. In consistency with this prediction, thresholds in the present experiment did *not* increase systematically across targets as they had in the previous three experiments. Rather, there was a trend in the opposite direction. Importantly, this effect resulted in a decrease in discrimination thresholds for the far targets in the high-salience conditions (2DotRef, LineRef) relative to performance in Experiment 3. By contrast, thresholds for targets close to the axes in these conditions were comparable across Experiments 3 and 4. Thus, it appears that neural activation associated with the presentation of the first stimulus dot can be repelled quickly (i.e., within 500 msec) from a nearby reference axis, enhancing discrimination performance when S2 is presented toward the axis.

Although results from this experiment support the second prediction of the DFT, one result was unexpected: Thresholds in the NoRef conditions were higher than those in Experiment 3. It is possible that the direction of S2 has a major effect in this condition, particularly on the close targets (cf. Figures 8 and 9). It is also possible, however, that the use of a pretest globally altered the baseline level of discrimination performance. In particular, results from Experiments 1–3 included data from several participants with low thresholds. Data from such "hyper-discriminators" were eliminated in this experiment. This would have the effect of shifting the baseline threshold up. Consequently, it is not clear whether thresholds in the NoRef conditions in the present experiment were higher than those in Experiment 3 because we manipulated the direction of S2 or because of the pretest. Importantly, this issue applies as well to data from the high-salience conditions: It is not clear whether thresholds to the close targets in the high-salience conditions were, in fact, comparable to those of Experiment 3. Given that results of the high-salience conditions bear most directly on the prediction of the DFT, we examined this issue more carefully in Experiment 5 by using a fully within-subjects design.

One final issue deserves comment. A secondary goal of this experiment was to increase the salience of the line display to investigate whether this would lead to further enhancement of position discrimination. As in the previous experiments, however, the two high-salience conditions did not differ. This suggests that a critical factor in the salience of the symmetry axes in our task space is the spatial separation of the two endpoints closest to the stimulus space (i.e., the two dots in the 2DotRef condition and the endpoints of the lines in the DotLineRef and LineRef conditions).

EXPERIMENT 5

Thus far, we have considered the two predictions of the DFT in isolation. Specifically, in Experiments 1–3 we examined the prediction that position discrimination would be enhanced due to narrowing activation profiles caused by increased inhibition with a more salient reference axis. In Experiment 4, we examined the prediction that the inhibitory gradient associated with the reference axes would contribute to fast repulsion effects. Critically, however, both effects have their origin in the reference-related inhibitory input to the model. Thus, according to the DFT, both effects are at work simultaneously. The primary goal of the present experiment was to test the fast repulsion prediction of the theory by manipulating the direction of S2 as a within-subjects factor. Importantly, however, the within-subjects nature of this experiment allowed us to test directly whether or not both inhibitory effects are at work simultaneously.

Consider what discrimination thresholds would look like if performance were influenced only by peak widths in the model. In such a case, the direction of S2 should not matter; only the separation of the targets from the reference axis should matter, with lower thresholds close to the axis, where peaks are narrower (see Figure 11A). Alternatively, if fast repulsion were the only contributor to reference-related enhancement effects, then performance to close targets should not differ with changes in the direction of S2 presentation, since repulsion here is minimal. Conversely, performance to far targets should differ dramatically with high thresholds when S2 moves away from the axis—in the direction of drift—and low thresholds when S2 moves toward the axis—in the direction opposite drift (see Figure 11B). Results of Experiments 1–3 when S2 was always presented away from the axes are consistent with both types of inhibitory effects (cf. dashed lines in Figures 11A and 11B). Thus, presenting S2 toward a reference axis provides a critical test of these two types of inhibitory effects. Nevertheless, the DFT predicts that *both* effects are at work. If this is the case, then performance in this critical condition should reflect a mixture of the two effects, as depicted in Figure 11C. In particular, when S2 is presented toward a reference axis, thresholds should be lower to the far target, but this reduction should be counteracted, in part, by greater peak widths far from the axis.
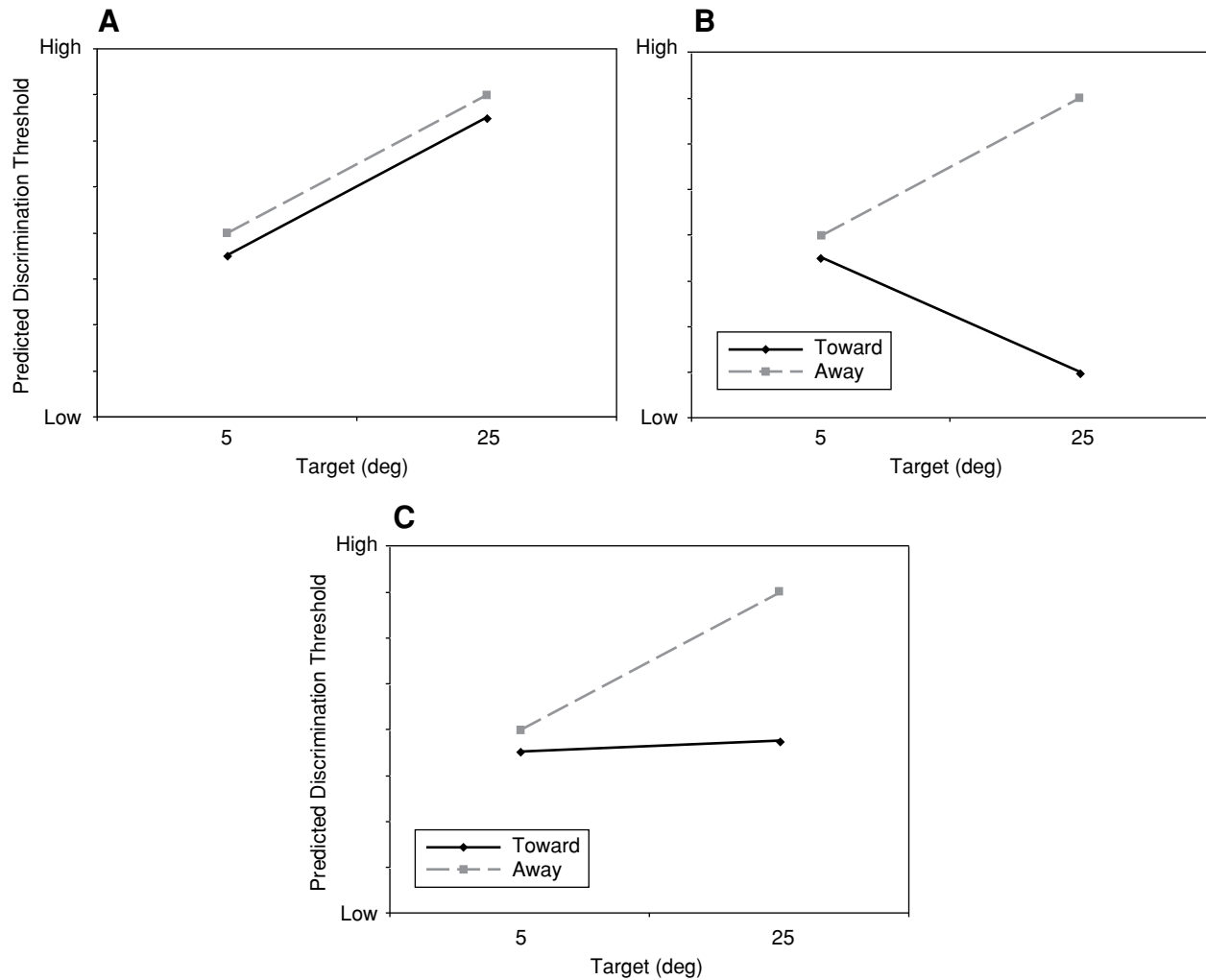
A

B

C

Figure 11. Predicted patterns of error for Experiment 5 based on peak width (A), fast repulsion (B), and both (C) for stimulus separations toward (solid lines) versus away from (dashed lines) the axis.

Thus, discrimination thresholds to the far target should be between the very low threshold depicted by the solid line in Figure 11B and the very high threshold depicted by the solid line in Figure 11A.

Method

Participants. The participants were 15 adults (8 females and 7 males, mean age = 19.9 years, SD = 1.2) with normal or corrected-to-normal vision. The participants received research exposure credit in an introductory psychology course for their participation. Each participant completed one session. Data from 2 additional participants were excluded for the following reasons: One participant did not complete all of the trials, and 1 participant did not meet the inclusion criterion (see Experiment 1).

Apparatus. In all details, the apparatus was identical to that used in Experiment 1.

Procedure. All procedural details were identical to those of Experiment 1 with the exception that the participants completed all trials in a single session (see Experimental Design, below).

Experimental design. Two of the six target locations from Experiment 1—5° and 25°—were used here because these targets provide a critical test of the DFT prediction. In addition, we included the

stimulus separations from both Experiment 3 and Experiment 4—that is, both targets were presented with S2 0–7 pixels toward the axis and 0–7 pixels away from the axis. For ease of analysis, we coded separations toward the axis as negative and separations away from the axis as positive. As in previous experiments, the participants completed 18 trials to each stimulus separation for each target, with one exception: The 0-pixel separation had double the number of trials (36) because this separation served as the starting point for both stimulus directions. Since all previous experiments showed little differentiation between the two salient perceptual displays, we used only the 2DotRef condition. Moreover, because Experiments 3 and 4 showed no effects of axis, the present study probed only performance around the midline axis.

Method of analysis. The method of analysis was identical to that used in Experiment 1, with one exception: Because S2 moved in either direction, we computed separate discrimination thresholds for each direction as well as for each target. In addition, we did not use the pretest that was established in Experiment 4.

Results

Figure 12 shows mean discrimination thresholds across targets and stimulus directions. Discrimination thresholds
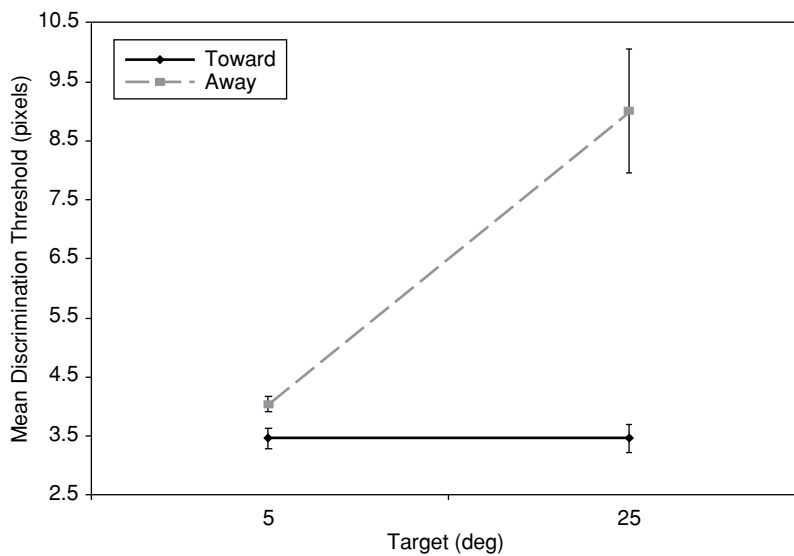
Figure 12. Mean discrimination thresholds across targets and stimulus directions in Experiment 5. Error bars represent one standard error.

for the close target (5º) were consistently low regardless of the direction in which S2 moved. By contrast, there was a large difference in thresholds to the far target across stimulus directions, with higher thresholds when S2 was presented away from the reference axis. Importantly, however, there was no difference in performance to the close and far targets when S2 was presented toward the reference axis. These data are consistent with the predictions of the DFT.

We analyzed these data in a two-way ANOVA with target (5º vs. 25º) and direction (toward vs. away) as within-subjects factors. This analysis revealed significant main effects of target [$F(1,14) = 6.65$, $p < .05$] and direction [$F(1,14) = 6.44$, $p < .05$]. These effects were subsumed by a target $\times$ direction interaction [$F(1,14) = 5.29$, $p < .05$]. Tests of simple effects revealed a significant effect of target only when S2 was presented away from the axis [$F(1,14) = 5.96$, $p < .05$].

Discussion

The goal of this experiment was to test the prediction of the DFT shown in Figure 11C. Results were consistent with the theory, suggesting that both types of reference-related inhibitory processes depicted in Figure 11 are at work in our task. Specifically, the activation profiles associated with stimuli presented near a reference axis are narrower than activation profiles associated with stimuli far from a reference axis (see also Kinchla, 1971). Moreover, these activation profiles are quickly repelled from reference frames during the short delays used here (500 msec), creating a dependency on the direction of S2 for targets far from the axis. These data provide strong support for the reference-related mechanisms captured by the DFT, suggesting that this theory offers a task-general view of spatial reference effects.

EXPERIMENT 6

Experiments 1–5 all tested targets presented on the right side of the axis. It is possible that this asymmetric distribution of targets relative to the reference axis produced attentional biases that contributed to our results. To address this possibility, Experiment 6 included targets on both sides of the axis in a design analogous to that of Experiment 5. The goal of this experiment was to verify that our results are indeed driven by reference axis effects, even when the target distribution is symmetric relative to the reference frame and when target location and the direction of stimulus separation are randomized. In addition, because the results of Experiment 5 showing the effects of both narrow peaks and fast repulsion provide a crucial test of the DFT, we wanted to replicate these findings and verify that they generalize to the other side of midline.

Method

Participants. The participants were 13 adults (10 females and 3 males, mean age = 20.6 years, $SD = 1.3$) with normal or corrected-to-normal vision. The participants were paid $10/h for their participation and completed three sessions, each on a different day. Data from 1 additional participant were excluded because she did not complete all of the sessions.

Apparatus. In all details, the apparatus was identical to that used in Experiment 1.

Procedure. All procedural details were identical to those of Experiment 1 with the exception that the participants completed three sessions (see Experimental Design, below).

Experimental design. The two target locations from Experiment 5 (5º and 25º) were used here, as were the same locations on the left side of the axis (-5º and -25º). As in Experiment 5, we used the 2DotRef condition around the midline axis, and all targets were presented with S2 0–7 pixels toward the axis and 0–7 pixels away from the axis. Again, we coded separations toward the axis as negative and those away from the axis as positive. As in previous experiments, the

participants completed 18 trials to each stimulus separation for each target, with one exception: The 0-pixel separation had double the number of trials (36) because this separation served as the starting point for both stimulus directions.

Method of analysis. The method of analysis was identical to that used in Experiment 5.

Results

Figure 13 shows mean discrimination thresholds across targets and directions. As can be seen in this figure, discrimination thresholds for the close targets ($-5°$ and $5°$) were consistently low regardless of the direction in which S2 moved. By contrast, there were large differences in thresholds to the far targets ($-25°$ and $25°$) across stimulus directions, with higher thresholds when S2 was presented away from the reference axis. Importantly, however, there were no differences in performance for the close and far targets when S2 was presented toward the reference axis. These data are consistent with the predictions of the DFT.

We analyzed these data in a three-way ANOVA with target (5° vs. 25°), direction (toward vs. away), and side (left of axis vs. right of axis) as within-subjects factors. This analysis revealed significant main effects of target [$F(1,12) = 15.095$, $p < .01$] and direction [$F(1,12) = 11.684$, $p < .01$]. These effects were subsumed by a target $\times$ direction interaction [$F(1,12) = 6.585$, $p < .05$]. Tests of simple effects revealed a significant target effect only when S2 was presented away from the axis [$F(1,12) = 10.547$, $p < .01$]. Importantly, there were no significant effects of side (all $ps > .6$).

To confirm that the same effects occur on both sides of the axis, we conducted planned comparisons using only responses to targets to the left side of the axis. This two-way ANOVA with target and direction as within-subjects factors revealed significant main effects of target [$F(1,12) = 37.979$, $p < .001$] and direction [$F(1,12) = 11.238$, $p < $

.01]. These effects were subsumed by a target $\times$ direction interaction [$F(1,12) = 11.250$, $p < .01$]. Tests of simple effects revealed a significant effect target only when S2 was presented away from the axis [$F(1,12) = 25.396$, $p < .001$]. These effects replicate those found in Experiment 5, in which only targets on the right side of the axis were tested.

Discussion

The goal of this experiment was to replicate and extend the findings of Experiment 5 in a condition in which targets were probed on both sides of the reference axis. We replicated the pattern of results from Experiment 5 regardless of whether targets were presented to the left or to the right of the axis. This suggests that modulations of performance close to and far from the reference axis relative to the direction of S2 are tightly linked to the reference frame rather than to an attentional bias that shifts relative to the target distribution. The replication of results from Experiment 5 provides strong support for predictions of the DFT.

GENERAL DISCUSSION

In the present series of experiments, we sought to test two novel predictions of our application of the DFT to the task of position discrimination. First, Experiments 1–3 showed that position discrimination is enhanced near symmetry axes and that increasing the salience of the reference axis further enhances performance. Second, Experiments 4–6 showed that the direction in which S2 is presented relative to both S1 and the reference frame modifies performance for targets far from the axis due to fast repulsion. In particular, location discrimination far from a reference axis is better when S2 moves toward the axis—that is, in a direction opposite repulsion away from
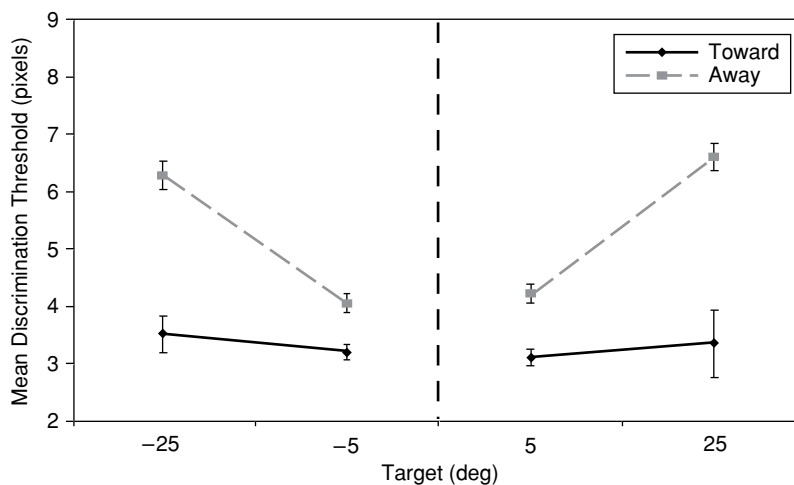

Figure 13. Mean discrimination thresholds across targets and stimulus directions in Experiment 6. Error bars represent one standard error. The dashed line indicates the position of the midline symmetry axis relative to the target locations.

the axis. In addition to these two predictions, in Experiments 5 and 6 we showed their combined effects, suggesting that reference-related enhancement and fast repulsion originate from the same inhibitory source as in the DFT.

Taken together, results from these experiments provide strong support for the DFT and, in particular, for the mechanisms proposed to underlie discrimination performance near reference frames. We know of no other model that makes the same predictions. Moreover, we know of no other model that can, a priori, explain the results of Experiments 1–6. Recall that Kinchla (1971) proposed a psychophysical model to account for enhanced discrimination near reference frames. According to this model, the encoding of each stimulus can be represented as a probability distribution with a variance influenced by both encoding noise and memory noise. Furthermore, Kinchla proposed that both types of noise are proportional to the separation between the stimulus and the reference frame. This model provides an account of the consistent enhancement effects near symmetry axes in our experiments; however, the model does not make a priori predictions about how varying the salience of reference frames would impact discrimination. Despite this, the salience effects reported here seem to fit into Kinchla's framework. It makes conceptual sense that encoding and memory noise would decrease with a more salient or higher fidelity reference signal. Clearly, though, it is important to formalize the link between the fidelity of the reference signal and the variance of the stimulus representations in this model. The second type of effect examined here—fast repulsion—is not consistent with Kinchla's model. There is no mechanism in this model for delay-dependent spatial drift away from a reference axis.

In summary, the DFT has a clear advantage over Kinchla's (1971) psychophysical model in that it provides an account of both salience and fast repulsion effects. The DFT also moves beyond the psychophysical account by positing a neurally plausible mechanism—reference-related inhibition—through which each of these effects arises. Although we had a behavioral focus in the present study, there are direct ties between the predictions of the DFT and neurophysiology. Recent approaches have demonstrated that activation profiles in dynamic fields can be directly estimated from firing rates of populations of cortical neurons using population coding ideas (Erlhagen et al., 1999). For example, the activation of neurons in motor cortex (e.g., Georgopoulos, Kettner, & Schwartz, 1988; Georgopoulos, Taira, & Lukashin, 1993), premotor cortex (e.g., di Pellegrino & Wise, 1993), and prefrontal cortex (e.g., di Pellegrino & Wise, 1993; Graziano et al., 1997; Wilson, Scalaidhe, & Goldman-Rakic, 1993) is broadly tuned in such a way that neurons respond maximally to stimulation at a "preferred" location and less vigorously as stimulation is moved away from the preferred location. A population representation can be constructed by lining these neurons up not according to their cortical locations, but according to their preferred spatial locations. Then, the activation of the newly aligned neurons in a spatial task can be plotted through time and the resulting activation profiles can be compared to profiles predicted by dynamic fields. These techniques have been used to directly observe, for instance, the representation of movement direction in motor and premotor cortex, providing evidence of preactivation of task-relevant spatial locations when precuing information is given (Bastian et al., 1998; Bastian et al., 2003). In addition to this population coding approach, the general principles of dynamic fields can be usefully integrated with a biophysical approach that attempts to incorporate the details of neurotransmitter action, timing properties of neurons, and so on (Compte et al., 2000).

Although the data presented here support the predictions of the DFT, several challenges remain for the theory. As it stands, the theory provides only a weak account of how *different* responses are generated. Recall that the model generates a response on the basis of whether or not activation pierces a threshold within a given window of time. In particular, a *same* response is generated when the threshold is pierced, whereas a *different* response is generated when the threshold is not pierced. There are two limitations of this theoretical approach. First, although the model can capture reaction times for *same* responses (i.e., the time it takes to pierce the response threshold; see Erlhagen & Schöner, 2002), it cannot capture reaction times for *different* responses. Second, our approach to *different* responses is not neurally realistic because this response is driven by the absence of activation rather than by its presence. We contend that these issues are solvable within the dynamic field framework, and the successful tests of the model presented here certainly motivate future efforts in this direction.

Another challenge for the DFT is to quantitatively capture the fast repulsion effects reported here while retaining the ability to capture spatial recall performance on a longer time scale (5- to 20-sec delays). This would more formally bind the time-dependent processes in the model across tasks and give us another way to examine whether or not the same reference-related processes operate at both short and long delays. In a similar vein, we are currently examining how the salience of reference frames modulates spatial recall performance, as well as whether or not there are within-subjects correlations between position discrimination and spatial recall performance near the same reference frames.

One of the primary motivations for this study was the desire to move toward a more task-general view of the processes that underlie reference frame effects in spatial cognition. Given that results support our claim that the DFT captures reference-related processes common to both position discrimination and spatial recall, the question arises as to whether this constitutes evidence of a task-general view. For instance, is it really so surprising that performance across spatial recall and position discrimination tasks is related given that these two types of tasks are similar? Although we agree that these tasks are similar at face value, they do have substantive differences that present challenges to theories that attempt to explain reference effects. In particular, position discrimination

operates on a much shorter timescale than the timescale used in most spatial recall tasks. Moreover, these two tasks require the generation of different response types. As evidence that these differences constitute substantive challenges, there are currently no models that attempt to link position discrimination and spatial recall despite the surface similarities of these tasks. In this context, it is notable that the DFT was able to predict subtle details of position discrimination performance in Experiments 5 and 6, despite the fact that this account was initially developed to capture spatial recall performance.

Although the present study represents an important achievement for the theory, future work needs to move more clearly beyond spatial recall and position discrimination. For instance, we have recently used the DFT to explain how people use perceived frames of reference in linguistic tasks, specifically addressing how people use the word *above* to describe visual displays (Spencer, Lipinski, & Samuelson, in press). In one task, for instance, participants were shown a target object at different angular separations from a vertical axis passing through a reference object and were asked to rate whether or not the target was *above* the referent (see also Hayward & Tarr, 1995; Logan & Sadler, 1996). Importantly, the participants gave their ratings when the target and the referent were visible (no delay) or after a 10-sec memory delay. Results showed that linguistic ratings are sensitive to the same reference-related repulsion effects examined in the present study. Specifically, targets that showed the largest delay-dependent errors in recall also showed a delay-dependent lowering of ratings, as if the target object had actually been presented farther from the referent and was, therefore, a poorer example of an *above* relation. Conversely, targets that showed little change over delay in recall also showed little change in ratings over delay. These results suggest that the reference-related processes captured by the DFT are indeed quite general, although at present the theory is not: Capturing performance in linguistic tasks requires substantive modifications (see Spencer et al., in press). Nevertheless, we contend that the DFT lays the foundation for thinking about the processes that give rise to reference frame effects in a way that cuts across traditional content areas in spatial cognition, thereby pointing toward a more integrative future.

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