Signal Strength Determines the Nature of the Relationship Between Perception and Working Memory

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Abstract

■ Neurophysiological and behavioral studies have shown that perception and memory share neural substrates and functional properties. But are perception and the active working memory of a stimulus one and the same? To address this question in the spatial domain, we compared the percept and the working memory of the position of a target stimulus embedded within a surround of moving dots. Motion in a particular direction after the target's offset biased the memory of target location in the same direction. However, motion simultaneous with a high-contrast, perceptually strong target biased the percept of target location in the opposite direction. Thus, perception and working memory can be modified by motion in qualitatively different ways. Manipulations to strengthen the memory trace had no effect on the direction of the memory bias, indicating that memory signal strength can never equal that of the percept of a strong stimulus. However, the percept of a weak stimulus was biased in the direction of motion. Thus, although perception and working memory are not inherently different, they can differ behaviorally depending on the strength of the perceptual signal. Understanding how a changing surround biases neural representations in general, and postsensory processes in particular, can help one understand past reports of spatial mislocalization. ■

Operationally, perception can be regarded as a representation in the brain of something currently or very recently present on the retina, and memory (disregarding otherwise important distinctions between different kinds of memories) as an internal representation of something that was shown in the past. Past studies have demonstrated vigorous interactions between perception and memory (Kerst & Howard, 1978; Kosslyn, Ball, & Resier, 1978) and have shown that perception and memory share several common functional properties (Ishai & Sagi, 1995a, 1995b) and apparently common representations in the brain (Kosslyn et al., 1999; Belger et al., 1998; Smith et al., 1995; Petrides, Alivastos, Evans, & Meyer, 1993; Bisaich & Luzzatti, 1978). Nonetheless, intuition suggests that some differences must exist between the mental processes that underlie perception and the mental processes or mechanisms that construct and keep active an internal representation of something consciously perceived earlier—processes that define working memory. In the present study on spatial working memory, an active form of visual short-term memory, we show just that. In particular, we demonstrate that the effects of visual context (surround motion) on spatial perception and spatial working memory can be similar or opposite, depending on the strength of the stimulus. We show that the

bottom-up, sensory signal of a physically present stimulus is powerful and robust, while the signal generated from postsensory internal mechanisms underlying working memory is not. A clear demarcation of sensory and postsensory mechanisms can better our understanding of perceptual effects, which we demonstrate with an example.

RESULTS

In Experiment Ia, a stationary, circular, high-stimulus energy target was displayed on a surround comprised of randomly located dots (see Methods). All the dots drifted horizontally—left or right depending on the trial—with constant, uniform velocity (Figure 1A, i). The target remained on the screen during the entire time the surround dots drifted (Figure 1A, ii). The observer's task was to judge the horizontal position (left or right?) of the target relative to that of a high-contrast reference marker located just above the moving surround and close to the fixation point (FP), and displayed during the last 90 msec that the target was on (Figure 1A, ii). It bears mention that the marker was briefly displayed while the target was still present, so judging the target's position relative to the marker was a perceptual task. The combined response over all observers (*n* = 4; one author and three naïve observers) is shown in Figure 1B for both the surround dots drifting right (black squares, black curve) and the surround dots drifting left conditions (open circles, gray

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Figure 1. Effects of concurrent and subsequent motion of the surround on the position judgment of a perceptually strong, stationary target. (A) Display (i) and timeline (ii) of a trial in Experiment Ia (perceptually strong target, concurrent motion). (B) Group responses ($n = 4$) over each of seven predetermined locations of the target relative to a marker are shown. The intersections of the vertical dotted lines with the two curves are the points of subjective equality (PSE), where the target appears to the left or right of the marker an equal number of times. Surround motion on the left (right) biased estimates rightward (leftward). (C) Display (i) and timeline (ii) of a trial in Experiment Ib (perceptually strong target, subsequent motion). (D) Group data ($n = 4$) from Experiment Ib are given. Surround motion on the left (right) biased estimates leftward (rightward). Note that the relative locations of left and right surround motion PSEs are reversed compared with those in (B).
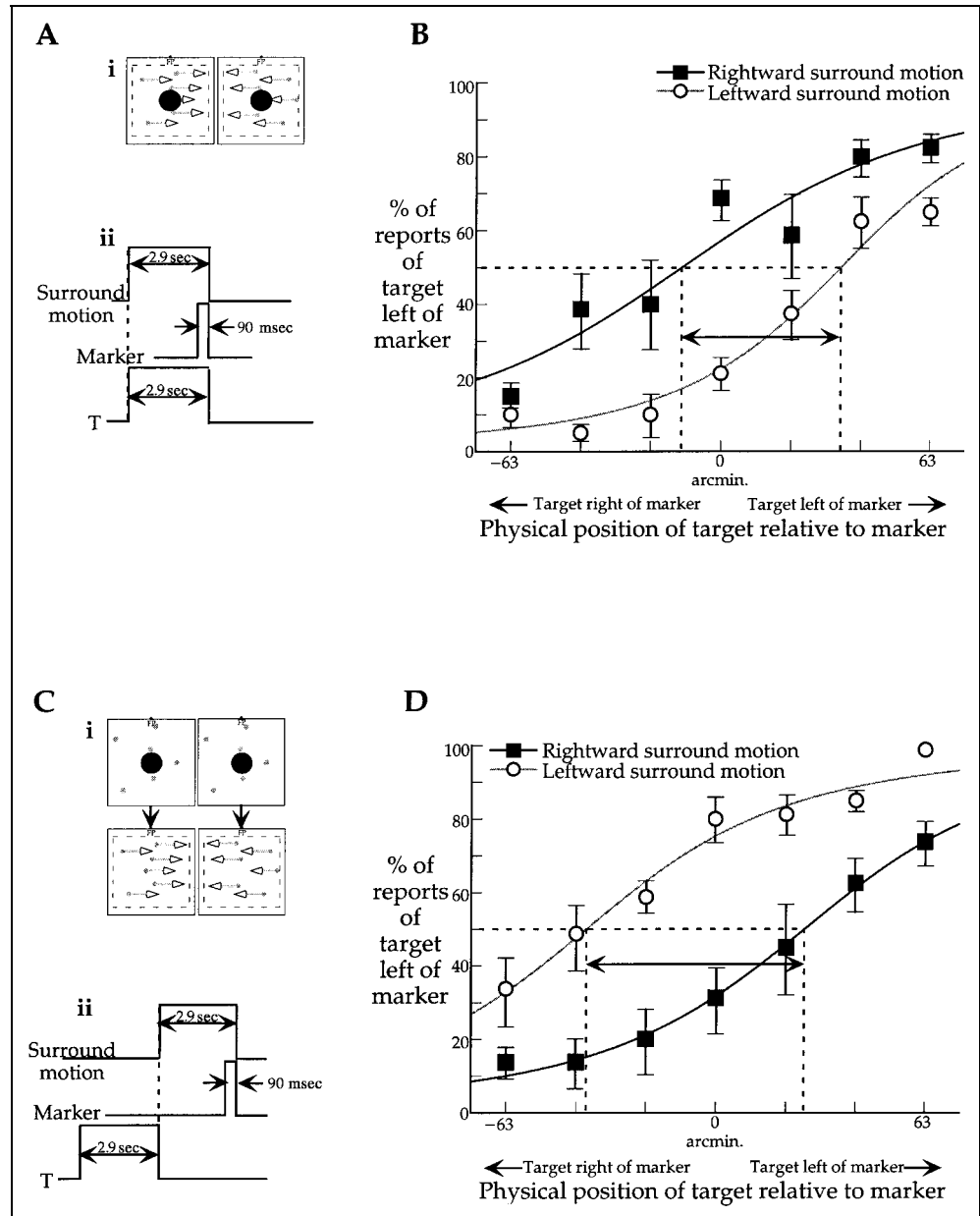
curve). The data were fitted with psychometric curves using probit analysis (McKee, Klein, & Teller, 1985; Finney, 1971). The magnitude of the bias is half the distance between the points of subjective equality (PSEs) defined under the two curves in Figure 1B (double arrow; −24 minutes of arc, or arcmin, negative values signify that the direction of the bias was opposite to that of the surround's motion). For each observer, the target was mislocalized in the direction opposite that of the motion of the surround (we call this effect "induced position," analogous with the perceptual phenomenon of induced motion; Duncker, 1938). The bootstrap method (Foster & Bischof, 1991) revealed the difference in threshold estimates (T_{50}) between the two psychometric functions was highly significant ($p < .001$; see Methods: Statistical analysis, for details).

Because the surround dots remained on the screen after the target's disappearance, one might argue that the internal representation of the target was dragged by a motion after effect (MAE) that followed the true motion but in the opposite direction, thereby accounting for the mislocalization. This is unlikely however, as 2.9 sec of motion is too short to generate a robust MAE (Wohlgemuth, 1911). Our own experiments with the MAE show that 30-sec- to 1-min-long motion is required to get a mislocalization of comparable magnitude (Sheth & Shimojo, 2000b). Finally, in a control experiment, we blanked the entire screen once the dots stopped moving. Because neither the dots nor the marker remained on after the target's offset, no MAE was possible. In spite of this, target position estimates were shifted in the opposite direction to the motion

($n = 2$; mean bias = −18 arcmin).[1] On the basis of these experiments and arguments, we conclude that the mislocalization was not caused by a MAE that might have followed the true motion.

In Experiment Ia, the task was to render a perceptual judgment of the target position. What if the task is to render a judgment based on working memory of the target position instead? Figure 1C and D, respectively, give the timeline and results of Experiment Ib. As before, the perceptually strong target was shown for the same 2.9-sec duration but the surround dots remained stationary (Figure 1C, i). The dots moved only after target offset, and the marker appeared in the last 90 msec of the 2.9-sec-long surround motion period. Thus, unlike in Experiment Ia, the marker came on more than 2.8 sec after the target was turned off. So judgment of the target's position relative to the marker could not be based on bottom-up sensory signals (Figure 1C, ii) or on iconic memory, which has a life span of less than 1 sec beyond sensory stimulation (Sperling, 1960). Instead, the judgment had to be based on an internal working memory representation of the target's spatial location. Figure 1D shows that these remembered target position estimates were displaced significantly in the direction of the subsequent surround motion (analogous with the perceptual phenomenon of motion capture, we term this ''position capture''; see also Corballis & Corballis, 1993). The bias (+33 arcmin) was in the opposite direction of the bias in Experiment Ia, which is depicted by the left–right reversals of the PSEs of the left and right surround motion functions in Figure 1D versus Figure 1B. The bootstrap method (Foster & Bischof, 1991) revealed that the difference in threshold estimates between the two psychometric functions in Figure 1D was significant ($p < .001$). In demonstrating that surrounding motion shifted perception and memory of target position in opposite directions, Experiment I provides evidence for a dissociation of perception and working memory (Sheth & Shimojo, 2000a).

Because the reference marker was transiently displayed, one might argue that the flashed marker, not the target, was displaced by the adjacent moving field (Whitney & Cavanagh, 2000). However, there are several reasons why this is highly unlikely. First, the marker was closer to the FP than was the motion field, which reduces flash mislocalization to near zero. Moreover, the surround did not move once the flashed marker was off; in later experiments (see Figures 4 and 5), we will show that the perception of a flashed stimulus is not displaced by motion concurrent with the stimulus but by motion after the target's disappearance. Also, in a control experiment, instead of comparing the target's position relative to some marker, observers had to use a computer mouse to indicate their estimate of target position. On the concurrent motion task modeled after Experiment Ia, estimates of all three observers (mean

bias ± *SEM* = −51 ± 12 arcmin) were biased in the direction opposite the motion, thus duplicating the result of Experiment Ia. On the subsequent motion task modeled after Experiment Ib, estimates ($n = 4$; bias = +26 ± 16 arcmin) were biased in the direction of the motion, duplicating the result of Experiment Ib. Similar findings in the no-marker motor task as in Experiment I suggest that the target, not the marker, was mislocalized in Experiment I. In an additional control experiment, we explicitly tested whether the marker was mislocalized. Observers ($n = 2$) had to judge the position of the marker relative to that of a foveal bar located more than 3° from the motion field (mislocalization by a remote motion field is near zero for separations >3°, Whitney & Cavanagh, 2000). Surround motion had no effect on marker localization (mean bias <1 arcmin). From the above experiments, we conclude that the target, not the marker, was mislocalized in our experiments.

How can Experiment I, which shows that perception and memory are dissociable under certain conditions, be reconciled with the common belief that perception and memory have many common characteristics (Ishai & Sagi, 1995a, 1995b; Mehta, Newcombe, & DeHaan, 1992; Bisaich & Luzzatti, 1978; Kerst & Howard, 1978; Kosslyn et al., 1978, 1999)? The question can be posed more directly. Can perception and memory be displaced in the same direction under a different set of conditions? In a past study in which subjects had to judge the direction of motion of a target motion embedded in a moving surround, perceived induced motion switched to motion capture when target signal strength was reduced (Murakami & Shimojo, 1993). We hypothesized that in replacing the high-contrast target of Experiment I with a low-contrast one in the next pair of experiments (Experiment II), the resulting reduction in stimulus strength should reverse the direction of perceptual bias. Other than the change in target contrast, Experiments Ia and IIa (Figure 2A and B) were identical, as were Experiments Ib and IIb (Figure 2C and D). As anticipated, perceptual estimates of the perceptually weak target in Experiment II were pulled in the direction of motion (Figure 2B). Bias magnitude was +17 arcmin, and was marginally significant ($p < .1$). In Experiment IIb, motion after the presentation of the weak target (Figure 2C) also biased judgments in the direction of motion (Figure 2D), and the mean bias magnitude (+30 arcmin) was highly significant ($p < .001$).

To sum up, motion in a given direction displaces the perceived location of a perceptually strong stimulus in the opposite direction. But, working memory of the perceptually strong stimulus, the percept of a weak stimulus, and working memory of the weak stimulus are all shifted in the direction of motion. It seems, therefore, that if the stimulus is of sufficiently high contrast, the perceptual signal will be strong and robust, whereas the strength of the working memory

Figure 2. Effects of concurrent and subsequent motion of the surround on position judgments of a perceptually weak, stationary target. (A) Display (i) and timeline (ii) of a trial in Experiment IIa (perceptually weak target, concurrent motion). The gray hue of the target signifies its lower overall luminance and contrast compared to Experiment 1. (B) Group data of four observers and the psychometric curves generated by probit analysis. Surround motion on the left (right) biased estimates leftward (rightward). (C) Display (i) and timeline (ii) of a trial in Experiment IIb (perceptually weak target, subsequent motion) were identical to the trials in Experiment IIa except for the lower luminance and contrast of the target in Experiment IIb. (D) Group data and psychometric curves from Experiment IIb. Surround motion on the left (right) biased estimates leftward (rightward).
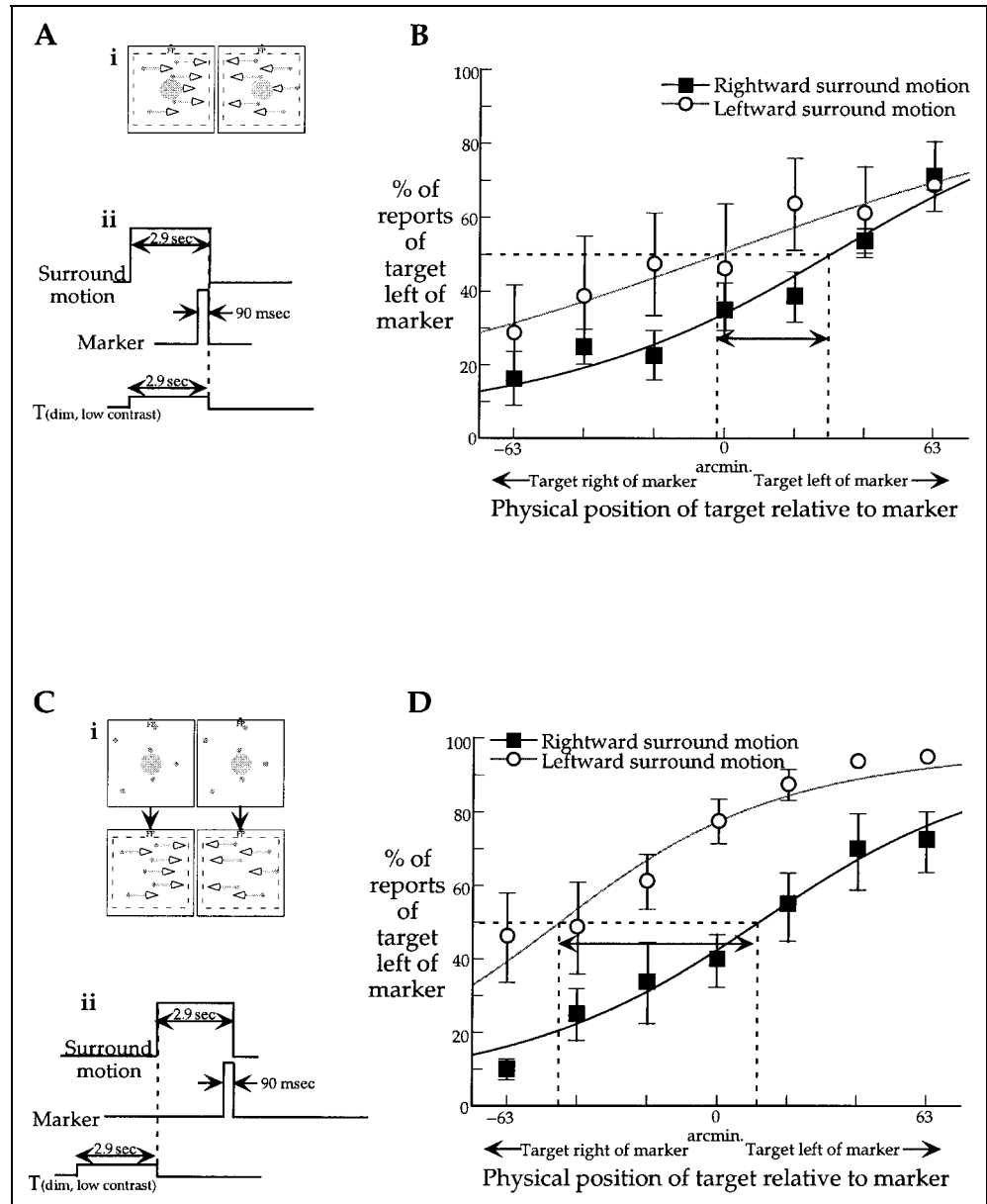
signal, regardless of the strength of the original perceptual signal, has an upper limit. Consistent with this, the memory error in the weak stimulus condition was larger than the corresponding perceptual error (compare Figure 2B and D), and the remembered positions of the low- and high-contrast targets were shifted by similar amounts in the direction of motion. That is to say, positional signals obtained from memory are invariably weak, and therefore susceptible to being biased in the direction of motion regardless of how strong is the original percept, or the memory trace.

There is a second possibility. If the memory trace is strengthened substantially, the bias in the direction of motion could be reduced considerably, or better yet, remembered judgments of position could shift in the opposite direction, as does the perception of a high-contrast stimulus.

Manipulations that presumably enhanced the strength of the memory trace indirectly (by enhancing the strength of the perceptual stimulus) or directly failed to reverse or reduce significantly the memory bias in the direction of surround motion, supporting the first hypothesis, namely, working memory is an invariably weak signal. In one experiment, we repeatedly blinked the stationary target on and off to reduce adaptation and refresh its neural representation (and also dimmed the surround dots to near-threshold levels in order to enhance target salience). In a second experiment, we fixed the actual location of the target on half the trials (target location was randomized on the other half), the rationale being that over many trials in which the target at the same location, memory for that location should enhance and become the equal of a perceptually strong stimulus in signal strength. In both experiments though,

estimates of remembered target position remained significantly shifted in the direction of motion supporting the first hypothesis.

To further generalize our findings, we investigated whether motion influences imagery in the same way that motion-influenced stimulus-derived memory (see Experiments Ib and IIb). In the imagery experiment, the observer must maintain in working memory the representation of a target never shown explicitly while the surround dots continue to drift. Given the difference in visual stimulation in the imagery experiment, a similar outcome to the one in the stimulus memory experi-

ments should confirm the generality of our hypothesis about memory. A set of four salient, stationary "target" bars were arranged on a static random dots background such that their imaginary extensions intersected at an imaginary point (Experiment III; Figure 3A, i). We asked participants ($n = 3$) to imagine an asterisk (to minimize contamination, the object to be imagined and the reference marker—a vertical bar—were kept different) centered on the imaginary intersection point. The rest of the experiment followed along the lines of previous memory experiments. The target bars disappeared, then the surround dots drifted, and finally the reference

Figure 3. Effects of surround motion on the stored position of an imagined target. (A) Display (i) and timeline (ii) of a trial in Experiment III (imagery). (B) Group data ($n = 3$) for both motion directions are given. For comparison, group data from the same three observers in Experiment Ib— the nonimagery counterpart— are given in the inset.
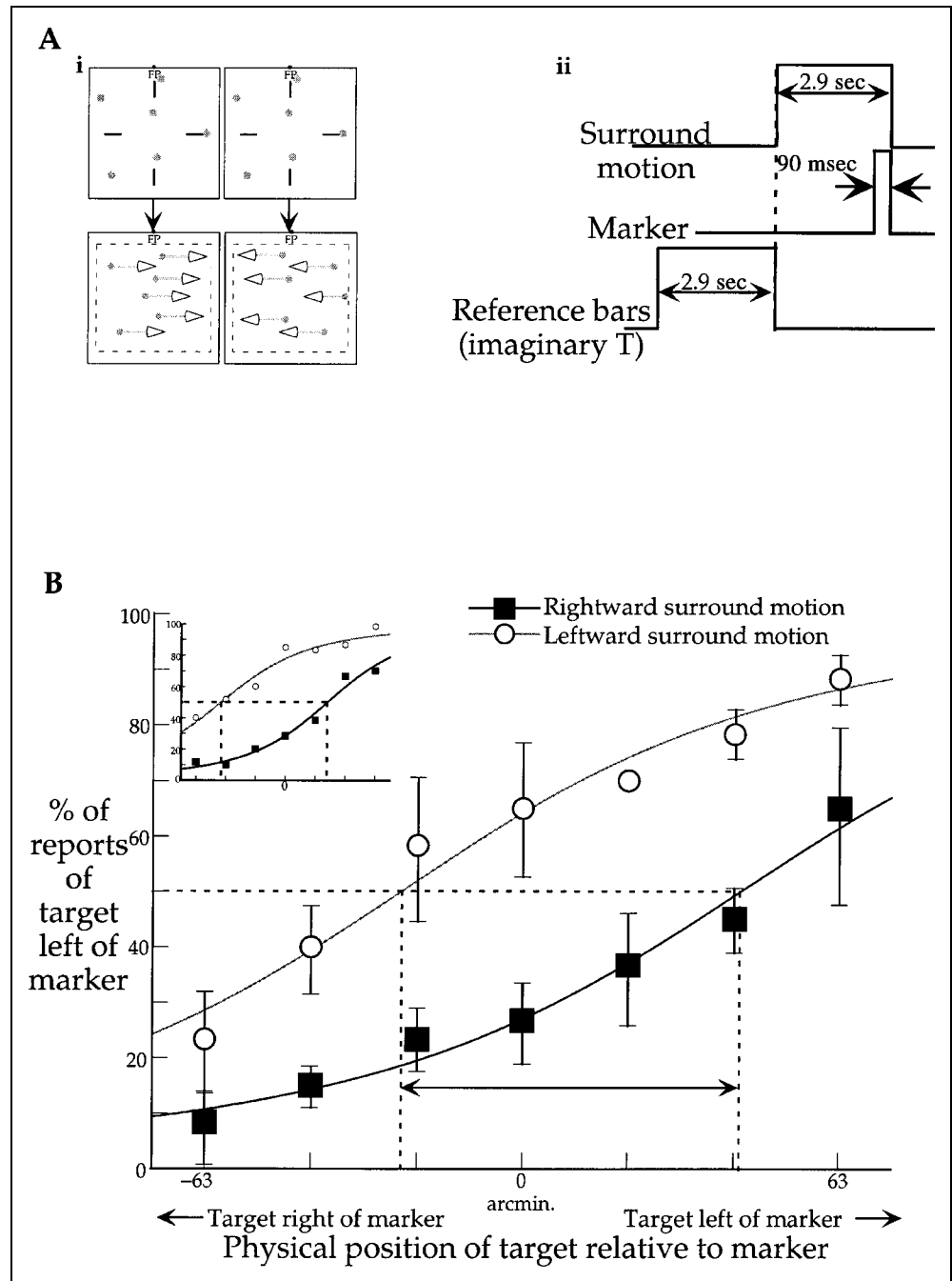
Figure 4. Effects of surround motion on the position judgment of a briefly displayed but otherwise salient (high-luminance, high-contrast) target. (A) Display (i) and timeline (ii) of a trial in Experiment IV (transient target experiment). The observer could respond only after the dots stopped moving. (B) Group data ($n = 5$) are shown. The target was mislocalized in the direction of motion.
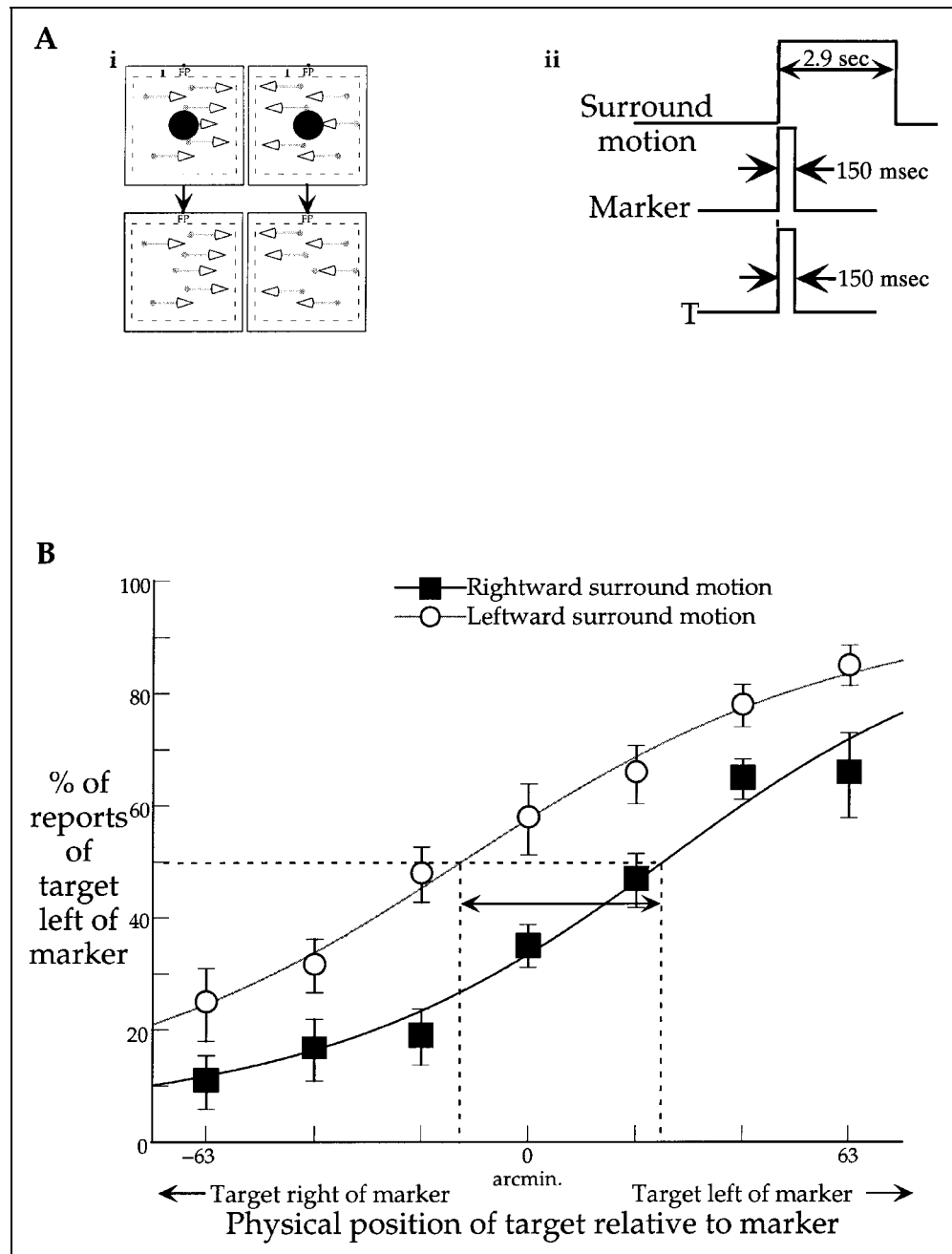
marker came on in the tail end of the motion (Figure 3A, ii). The observer's task was the same as before: To judge the remembered position of the imagined target relative to the visual marker. Position estimates of the imagined target were found to be biased in the direction of motion (Figure 3B, mean bias = +34 arcmin, $p < .001$). For comparison, pooled data from the same three participants on the stimulus memory task (Experiment Ib) are shown in Figure 3B, inset (mean bias = +37 arcmin in Experiment Ib). Both direction and magnitude of the mislocalization in the imagery and stimulus memory experiments were similar, qualitatively and quantitatively. The parallels in data indicate that imagery, like explicit stimulus memory,

is weak, in agreement with our own assertion that memory can never equal a perceptual stimulus of high strength.

The remarkable agreement in bias direction in all of our memory experiment data signifies that under diverse experimental manipulations, memory continues to be biased in the direction of motion, indicative of a representation of low signal strength. Thus, our work provides evidence for the idea that a weak percept has a behavioral analog in working memory (Experiment II), but a strong percept does not (Experiment I).

We assert that signal-strength-based dissociation between perception and active memory, or more generally, between sensory and postsensory processes

(includes iconic memory, a component of perceptual processes) can reshape our understanding of the mechanisms underlying well-known spatial localization phenomena (Whitney & Cavanagh, 2000; Nishida & Johnston, 1999; Snowden, 1998; Freyd & Finke, 1984).

To illustrate our point, we will analyze the phenomenon of motion capture and the accompanying mislocalization of target position (Whitney & Cavanagh, 2000; de Valois & de Valois, 1991; Ramachandran & Anstis, 1990). Motion capture occurs when a briefly flashed stationary target embedded within a moving surround is perceived to shift in the direction of motion. Experiment IV investigates whether motion capture systematically displaces estimates of target location in our paradigm. Compared with Experiment Ia, two stimulus parameters were changed. One, target duration was shortened to 150 msec, and two, reference marker and target were presented synchronously (Figure 4A). In accord with previous studies, but not with Experiment Ia of the present study, observers' ($n = 5$) estimates of perceived target position were significantly shifted in the direction of the surround motion (Figure 4B, mean bias = +20 arcmin, $p < .005$). The direction of mislocalization was opposite that observed in the high-contrast target perceptual task (Experiment Ia). In Experiment Ia, surround motion ceased the moment the target was turned off, whereas in Experment IV, the surround continued drifting. Could this difference in timing account for the difference in the outcomes of the two experiments? In other words, could motion following the target presentation account entirely for the mislocalization in the motion capture paradigm?

Figure 5. Varying the timing of surround motion relative to target presentation and its effect on position judgment. (A) Display (i) and timeline (ii) of a trial in Experiment Va (synchronous motion and target presentation). (B) Group data ($n = 3$) are shown. For the sake of comparison, data from Experiment IV for the same three observers are given in the accompanying inset. (C) Display (i) and timeline (ii) of a trial in Experiment Vb (target displayed at tail end of motion). (D) Group data ($n = 4$) are shown. For comparison, the inset gives Experiment IV data from the same four observers.
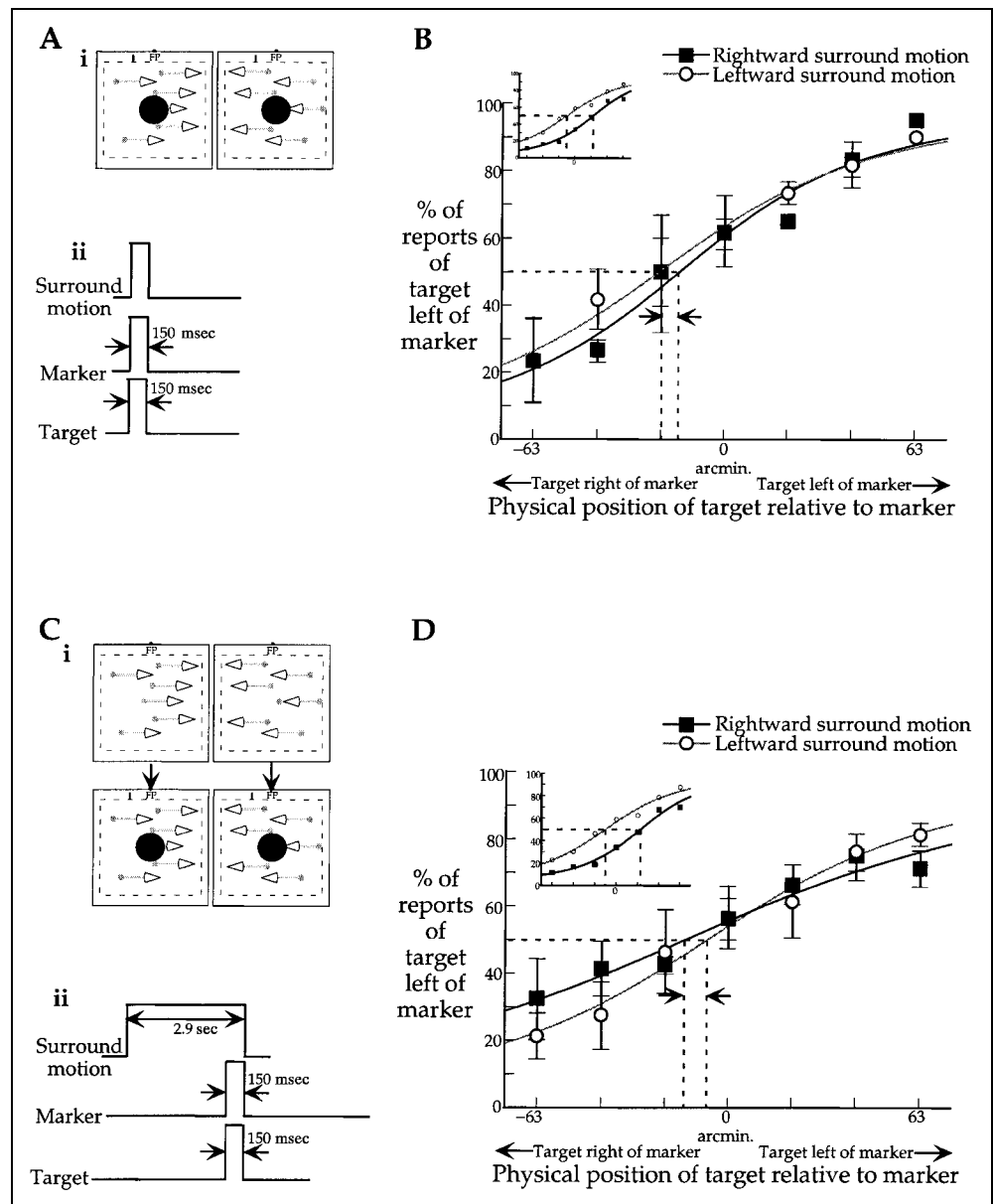
We addressed this question by stopping all motion after the target's offset and seeing whether mislocalization was eliminated. In Experiment Va, target and reference marker appeared at the start and remained on for 150 msec. Unlike Experiment IV, however, the surround dots stopped moving upon target offset (Figure 5A). The design thus isolated the effect of motion to when the target was physically present. In this case, the motion shifted target position estimates negligibly (Figure 5B, mean bias = +3 arcmin, $p > .55$, $n = 3$). Figure 5B, inset, shows data from the same three observers in Experiment IV for comparison. In a second experiment we allowed the surround to move for the 2.9-sec period as in Experiment IV, but presented the target (and the marker) in the last 150 msec of it (Experiment Vb). All other parameters assumed Experiment IV values (Figure 5C). Again, motion did not bias observers' ($n = 4$) target position estimates at all (Figure 5D, mean bias = −3 arcmin, $p > .6$). Thus, based on Experiments IV and V, motion of the surround did not distort the perceived target position while the target was present on the screen. Rather, motion after the target was offset displaced a postsensory iconic memory representation of the target, a representation that is presumably incorporated into the percept. We believe that the same general rule applies in other phenomena (Nishida & Johnston, 1999; Snowden, 1998; Freyd & Finke, 1984). A changing context can modify a signal of weak strength, and short-term working memory and postsensory processes (i.e., iconic memory) are signals of weak strength.

DISCUSSION

The present study shows that perception and working memory can be similar or dissimilar depending on the strength of the perceptual stimulus. For low stimulus strengths, perception and working memory are biased in the same direction by motion of the surround. For high stimulus strengths, memory is biased as before, but perception is either biased in the opposite direction or not biased at all. Experiments using blinking targets on backgrounds with barely visible dots, or a target presented at a fixed location throughout the session, or target imagery all yielded data indicating the memory signal simply cannot be robust enough to ever be the equal of a perceptual signal of high strength. On the other hand, a perceptually weak stimulus can be the equivalent of working memory in terms of what effect motion has on it. Thus, perception and working memory are not intrinsically different, as others have argued (Ishai & Sagi, 1995a, 1995b; Bisaich & Luzzatti, 1978; Kerst & Howard, 1978; Kosslyn et al., 1978, 1999), but they do, under certain conditions, differ behaviorally because of differential signal strengths.

A slightly different account of our data considers perception and working memory to be two separate but interconnected systems. If the target has high con-

trast, the perceptual system dominates, so when the surround moves, the representation is displaced against the direction of motion. If the target has low contrast or if it is absent, the representation in working memory dominates and the representation is displaced in the direction of motion. This account differs from the previous one in the supposition that working memory, and not the perceptual system, is used even when the stimulus is visible and being perceived, for example, in the low-contrast stimulus condition.

Single-unit recordings in macaque PFC and PC (Chafee & Goldman-Rakic, 1998; Mazzoni, Bracewell, Barash, & Andersen, 1996; Funahashi, Bruce, & Goldman-Rakic, 1989) have shown that "memory" neurons in the PFC often have significant "perceptual" activity (fire when the stimulus is on), suggesting a continuum between perception and memory in the physiology. Conversely, exclusively "perceptual" neurons have also been found within the same recording area in which memory neurons were found, which seems more compatible with the alternative notion that memory and perception are two separate but interconnected systems.

In spite of their subtle differences, both accounts recognize signal strength as the key parameter and both imply two modes of processing—one for strong signals and another for weak signals, including memory. Indeed, it is conceivable that the brain uses different strategies to process stimuli of different strengths. If the stimulus is perceptually salient and unambiguous, the neural activity possibly has a sharp peak in the location of the stimulus in the brain map, which would determine the judged location. On the other hand, if the stimulus is ambiguous and weak, a winner-take-all mode may not suffice. In order to boost the signal, the brain may need to pool activity over the map over several processing cycles, and then take the center of the pooled activity as the location of the stimulus. As a result, neighboring locations activated in the direction of motion will distort the judged activity center in the motion direction. Switching modes to an averaging strategy and maintaining activity over time for pooling both may require feedback from higher areas, and could potentially explain the involvement of higher areas (prefrontal cortex [PFC] and parietal cortex [PC]) in spatial memory tasks in humans (Belger et al., 1998; Smith et al., 1995; Petrides et al., 1993).

That activity in the delay period between stimulus offset and response is elevated above spontaneous levels in "memory neurons" (Chafee & Goldman-Rakic, 1998; Mazzoni et al., 1996; Funahashi et al., 1989) demonstrates that memory is stored as active neuronal activity. By showing that memory of target location is altered by surround motion, we lend psychophysical support to the prevailing notion that memory is an active reconstruction. Furthermore, our work on how ongoing motion alters remembered position implies that active, working memory, once created, does not simply fade over time in

an autonomous or undirected fashion, but interacts vigorously with ongoing perceptual signals (Sheth & Shimojo, 2001). Being labile (Nader, Schafe, & Le Doux, 2000), active memory distorted by the perceptual signals as a consequence. Thus, active memory bears the imprint not only of the perceptual input that created it but also of all perceptual events from its inception to its eventual retrieval (Sheth & Shimojo, 2000a).

Our study differs markedly from other reports on the effects of motion on judgments of target position (Whitney & Cavanagh, 2000; Nishida & Johnston, 1999; Snowden, 1998). These studies showed how motion influences the "perceived" position of a stationary object that is either coincident (Nishida & Johnston, 1999; Snowden, 1998) or noncoincident (Whitney & Cavanagh, 2000) "in space" with the motion. In contrast, our study shows how motion influences the "perceived" and actively "remembered" positions of a stationary object that are, respectively, coincident and noncoincident "in time" with the motion. Nonetheless, our work, which suggests memory (postsensory processes, more generally)—no matter how salient—never rises to the level of a perceptual stimulus of high signal strength, and which shows that changing context affects high- and low-strength signals differently provides a common framework for all such studies (Whitney & Cavanagh, 2000; Nishida & Johnston, 1999; Snowden, 1998; Freyd & Finke, 1984). A case in point, it was earlier believed that the MAE is not accompanied by a shift in the perceived position of the pattern being viewed (Nakayama, 1985; Gregory, 1966). However, there are recent reports of an illusory shift in position in the direction of the perceived MAE (Nishida & Johnston, 1999; Snowden, 1998). In the Nishida and Johnston (1999) study, a windmill pattern, whose segments differ minimally in contrast from their immediate neighbors, was used, and in the Snowden (1998) study, postsensory processes were biased. Therefore, in both studies, the signals that were displaced in space by the motion were weak—congruent with the themes of the present study.

Akin to our work on spatial memory, studies of high-level cognitive visual memory have found that postevent information becomes inextricably integrated into the original memory and irreversibly distorts it (Loftus & Palmer, 1974). In conjunction with those studies, our study showing distortions in low-level, visual spatial memory (see also Sheth & Shimojo, 2001) implies a surprising universality to memory dynamics. Studies of high-level visual memory have been criticized on the grounds that high-level distortions occur only in the retrieval process, not in the memory itself. That is to say, cognitive factors related to selection (response) can explain the distortions (Palmer, 1999; Riley, 1962). The low-level, precognitive nature of the spatial memory in the present study precludes this confound.

In conclusion, the strength of the perceptual stimulus determines the relationship between perception and working memory. Experiments under a variety of conditions suggest that memory is at best, only a faint echo of the actual percept and never the equivalent of a vivid, strong percept. Realizing how changing contexts bias memory and postsensory processes may go a long way in understanding many a "perceptual" phenomena too.

METHODS

Common Stimulus and Task Parameters

All stimuli were presented on a Sony Trinitron monitor (size: 37.5 × 30 cm, 75 Hz refresh) under control of a MAC PowerPC running MATLAB (Mathworks) and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Viewing was binocular. Room lights were turned off, and the observer had to maintain gaze on the FP throughout the trial. The observer's head was partially immobilized by means of a chin- and headrest placed 28.5 cm (1 cm = 2° of visual angle) from the computer monitor. The target subtended a diameter of 0.65° of visual angle. The surround consisted of a full field of 10,000 randomly placed dots, and occupied the entire screen. The mean dot density across the monitor was approximately 2.3 dots/degree^2. The dots were both smaller in size (11 arcmin diameter each) and of lower luminance (0.39 cd/m^2 each) than the target. Only dots within a central 40° × 40° area moved (100% coherence, 6.0°/sec speed) whereas the dots outside this area remained stationary. The direction (left/right) of horizontal background motion was randomized on every trial. The fixation point (FP) was always at the top of the screen, 5 cm above the central area of moving dots. Across trials, the horizontal coordinate of the target was randomly chosen from a predetermined range ([−10°, 10°]) on either side of the FP, and the vertical coordinate was in a range [26°, 34°] below the FP. The unusually short viewing distance and large target eccentricities served several purposes. One, the observer had to pay attention to perceive the target (lack of attention attenuates the effect). Two, in the case of a low contrast or briefly presented target, its large eccentricity rendered it much less salient than it could have otherwise been in the fovea. Three, the eccentricities were too large for the observer to even inadvertently saccade to the target from the original FP. After stimulus offset and upon hearing a beep, the observer had to respond by pressing one of two adjacent keys on a computer keyboard as to whether the target was left or right of the reference marker (1° long × 0.05° wide) presented just above the moving field. In separate but randomly interleaved trials, each stimulus sequence was run with all the surround dots drifting either left or right. This compensates for any selection bias on the observer's part. The horizontal coordinate of the reference marker relative to the target was chosen from one of seven prespecified, equally spaced values—one marker horizontal coordinate the

exact same as the target, and three each left and right of the target of linearly increasing physical distance from it. On a given task, each observer (chosen from a pool of nine volunteers: one author, the rest naive) ran 20 trials/motion direction (2)/point (7), for a total of 280 (20 × 2 × 7) trials. Each experimental session typically lasted 50–55 min, not including breaks.

Experiment Ia (Perceptually Strong Target, Concurrent Motion)

The stationary target (2.9-sec duration, nearly 100% contrast, 53.3 cd/m^2 luminance) was embedded on a dark screen (<0.01 cd/m^2 luminance with no dots turned on) containing randomly placed dots, each of luminance 0.39 cd/m^2. The central area of dots (indicated by the dashed border shown here for illustrative purposes only) drifted during the entire time the target remained on, while the dots outside the central area remained stationary. Ninety milliseconds before the target was to disappear and the dots were to stop moving, a bright, short vertical bar (marker) was randomly shown above the moving surround on the screen with equal probability from a set of seven predetermined horizontal coordinates. Upon disappearance of target and marker and simultaneous cessation of dot motion, the observer reported, in a self-paced manner, whether the target appeared left or right of the marker in a forced-choice paradigm.

Experiment Ib (Perceptually Strong Target, Subsequent Motion)

The stationary target (4.8 cd/m^2 and 84% luminance contrast) stayed on for 2.9 sec on a background of randomly placed static dots (background luminance minus the dots was 0.4 cd/m^2). Once the target was extinguished, the dots began drifting. Ninety milliseconds before the end of the motion, the marker appeared. Once the motion stopped and the marker was turned off the same instant, the observer could respond at any time.

Experiment IIa (Perceptually Weak Target, Concurrent Motion)

Parameters and experimental procedures were identical to that in Experiment Ia with the sole difference being the lower luminance (4.8 cd/m^2) and contrast (84%) of the target.

Experiment IIb (Perceptually Weak Target, Subsequent Motion)

Parameters and experimental procedures were identical to that in Experiment Ib with the sole difference

being the lower luminance (4.8 cd/m^2) and contrast (84%) of the target.

Experiment III (Imagery)

Four bright (53.3 cd/m^2 luminance) stationary bars (dimensions: 2° × 0.03°) were displayed for a duration of 2.9 sec on a static random-dots surround (background luminance <0.01 cd/m^2). The observer had to imagine a target shaped as an asterisk centered on the extrapolated intersection point of the bars. As in Experiments Ib and IIb, once the target was turned off, the dots in the central dashed area began moving coherently left or right for 2.9 sec. A marker was shown for 90 msec before the motion was to stop (task was the same as in prior experiments).

Experiment IV (Transient Target)

The target (53.3 cd/m^2 luminance, nearly 100% contrast) and marker were displayed during the first 150 msec of the 2.9-sec-long surround motion. After the dots stopped moving, the observer could indicate his/her judgment of the target's horizontal location relative to that of the marker.

Experiment Va (Synchronous Motion and Target)

Target parameters were identical to Experiment IV. The surround (dots lying within the dashed borders) drifted randomly left or right for 150 msec only. During this entire time the target and marker were displayed. As before, the observer could respond after the dots stopped moving.

Experiment Vb (Target Displayed at Tail End of Motion)

The surround drifted randomly left or right for 2.9 sec, just as in Experiment IV. The target and marker appeared for the last 150 msec of the motion. The target and marker disappeared, and the dots stopped moving—all in the same instant. The observer could respond thereafter.

Statistical Analysis

Computer simulations using a bootstrap method (Foster & Bischof, 1991) to test the significance of the difference in the two thresholds (left and right motion) enumerated all possible pairs of psychometric functions from the pooled distribution (right and left surround motions averaged) and weighted them by their binomial probability. Each of the possible pairs of psychometric functions yielded a pair of threshold estimates. The distribution of the threshold differences between the pairs of psychometric functions generated using the

bootstrap method was compared with the difference in threshold between the two psychometric functions $[T(\text{right})_{50} - T(\text{left})_{50}]$ in each experiment. The upper and lower threshold difference values of the distribution that would exclude the upper and lower 0.5% of the bootstrapped population, respectively, were taken as the 99% confidence limits. Using this technique, we can find out whether or not the threshold difference between the two psychometric functions in a given experiment fall outside of the confidence limits ($p < .01$).

Note

1. Experiment Vb furnishes additional evidence against the MAE account. In Experiment Vb (see Figure 5C), motion duration was the same as in Experiment Ia. Hence, MAE magnitude should be the same. Yet, there was no bias in the direction of the MAE in Experiment Vb (see Figure 5D), implying that the bias observed in Experiment Ia was not the result of an MAE.

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