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In space, the past can be recast but not the present

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Abstract. We address the relationship between perception and spatial, working memory. Specifically, we argue that perceptual experience following the creation of a representation of target location affects it in a systematic way. We designed a motor task in which observers had to point to the initial or final position of a horizontally drifting target embedded in a vertically drifting background. The target was perceived as having an illusory motion component in a direction opposite that of the inducer dots [Duncker, 1938, *Source Book of Gestalt Psychology* (London: Kegan Paul, Trench, Trubner and Co)]. For both positions, there was an identical time delay before the observer could respond. Nonetheless, estimates of the initial target position were significantly biased by the illusion in a direction opposite the perceived target motion, and both bias and variability were significantly greater than those of the target's final position. In prior studies on positional accuracy with induced displacement, a delay before a pointing response led to an unbiased position estimate obtained without delay to become biased, leading investigators to argue for a long-lasting, inaccurate cognitive system that overrules an accurate, nonetheless transient, motor one (Bridgeman et al, 1997, *Perceptual Psychology* **59** 456 – 469). Since the same motor task with identical delay on either position yielded different outcomes, a hypothesis based on distinct motor and cognitive representations of visual space is untenable here. Instead, we argue that an online representation of the target's original position is updated in an ongoing fashion in order to reconcile the perceived illusion with the veridically perceived present (current target

1 Introduction

Consider a common, everyday situation wherein one observes the initial position and subsequent movements of an object. Would the spatial representation of the initial position be influenced by the ensuing movement? Assuming independence of the representation from perception, one would predict no influence. But, if dynamic interactions are assumed between the representation and perception, a vigorous influence might be expected. Indeed, in preliminary experiments, when observers had to judge the initial position of a target undergoing induced motion, ie illusory target motion in the direction opposite the moving field, localizations were biased opposite the perceived target direction (Sheth and Shimojo, unpublished observations). However, localization judgments of the target's terminal position did not yield a similar, systematic bias. There were two possible interpretations of the discrepancy in the data between the two positions. Since the target was on for a few seconds, there was a comparatively shorter delay before observers could point to the final position (the observer could respond instantaneously after the target offset). Hence, a difference in the time interval between stimulus and response could explain the discrepancy, consistent with induced displacement reports of a delay-dependent dissociation within the motor system (Bridgeman et al 1997). Alternatively, the illusion was seen after the target came on, thus had a chance to affect the initial position, but not after it was turned off. This difference may be key, therefore differences in time may not be that critical. To rephrase, working memory of target location (or its active, online, spatial representation) may be biased by later perception (induced motion illusion). We examine the plausibility of this hypothesis here.

1.1 *Prior induced motion/displacement studies in normal humans*

There have been several studies of positional accuracy in induced motion or induced displacement. In Bridgeman et al (1979), a stimulus was displaced and observers had to detect the displacement. It was shown that, even if the displacement were not perceived, observers could still point to the center of the displaced stimulus just as accurately as when they perceived it. In a related study (Bridgeman et al 1981), a target was either physically displaced or remained stationary while a background stimulus underwent stroboscopic induced motion. Again, whether or not the target was displaced, the background could not significantly bias estimates of the last target position. On the basis of these studies, Bridgeman et al argued for the existence of separate perception and action systems. Observers in Bridgeman et al (1997) had to point to the position of a target located inside an off-center frame. Motor behavior of some observers immediately following stimulus offset was unbiased. However, when delayed, the motor response did show a Roelofs effect—a tendency to judge the target in the direction opposite the offset of the frame—explained by proposing a transfer of spatial information from the cognitive system into the motor one. Other studies have also shown that time delays adversely affect mechanisms in the brain subserving action (Wong and Mack 1981; Abrams and Landgraf 1990). Thus, there is a delay-dependent dichotomy: when action is immediate, positional estimates are unbiased and accurate, but adding a delay reduces accuracy and biases motor estimates, in accordance with the percept.

1.2 *Could future perceptual events affect spatial, working memory?*

Careful analysis of the above reports reveals a common thread in the methodology: observers were tested on the target's final position only. In all these studies, there was no new perceptual experience (say, an evolving illusion) after the target reached its final position. In the case of induced target motion, the target needs to be present in order to perceive the illusion. Hence, the illusion will cease the instant the target is turned off. Thus, these studies could not test the issue whether spatial, working memory (active, spatial representation) of the target's position could be influenced by subsequent perceptual experience. To this end, non-terminal target locations need to be estimated, as in our preliminary study described above. If subsequent perception does affect spatial representation of the target's position, the illusion must bias pointing to non-terminal positions in the target's trajectory, but not pointing to the target's last position. On the basis of the delay-dependent dichotomy studies described above, if the motor response were delayed equally on different target positions, accuracy of pointing should be the same irrespective of position, since either the cognitive map will supplant the sensorimotor map and bias the pointing behavior about the same, or pointing will remain unbiased in case the delay is small. We tested the merits of our hypothesis, namely that perceptual events distort the spatial, working memory (active, spatial representation) of target location, in a series of experiments.

1.3 *General experimental paradigm and predictions*

On a background of vertically drifting dots, a target drifted horizontally with uniform velocity (figure 1a). Typically, the target appeared to have a vertical motion component in a direction opposite that of the dots. For example, when superimposed on a background of dots streaming down, a target moving right appeared to move up and to the right (figure 1b). This illusion is termed induced motion or the Duncker illusion (Duncker 1938). Once the stimulus (target and dots texture) disappeared, observers had to point to either the location where the target came on (initial position), or where it was last present before its offset (terminal position). The delay between stimulus (initial/final target position) and motor response was kept the same for both positions throughout.

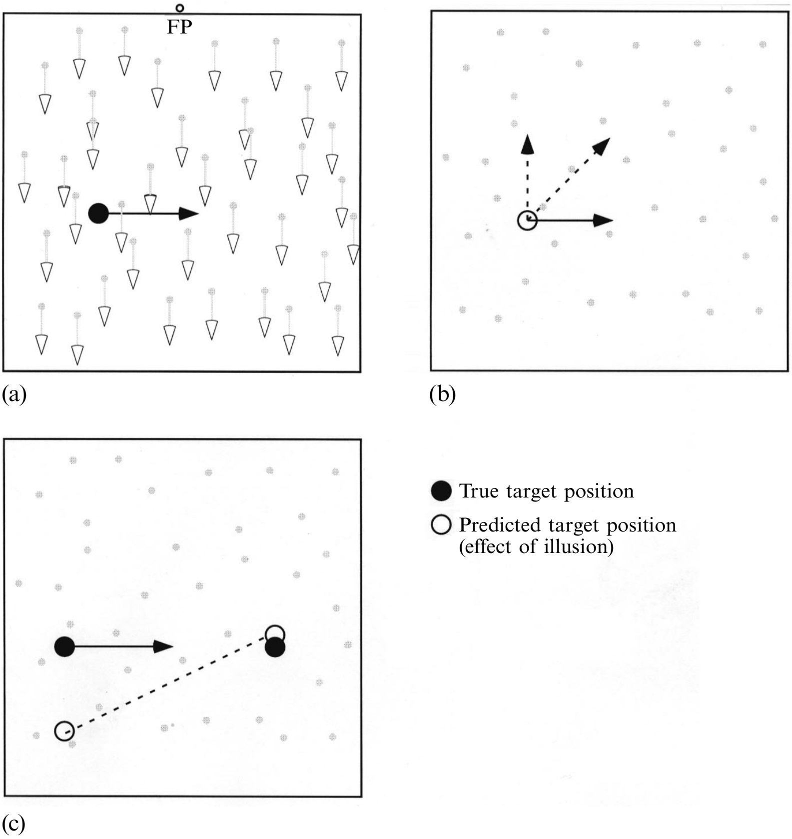


Figure 1. The stimulus display, the observer's perception of induced motion, and predicted pointing error. (a) A display of random dots constituted the background. All the dots drifted vertically up/down with uniform velocity. A target, which was of higher contrast and larger size than the dots, moved left/right with uniform horizontal velocity. The observer had to maintain gaze on a fixation marker located just above the monitor (FP). (b) The observer typically perceived the target drifting in a diagonal direction. This motion is the vector sum of the target's true, horizontal motion (solid lines), and illusory, vertical motion (dashed lines) opposite in direction to that of the true (vertical) motion of the dots. (c) We predict that the illusion of vertical target motion leads to a systematic error in the localization of the target's vertical coordinate. The observer's error in localizing the target's initial vertical coordinate (left) should be biased in the direction of the target's illusory motion. Localization of the target's post-illusory, terminal location should be relatively unbiased.

We offer an alternative scenario to the delay-dependent dissociation view. Both starting and ending points in a target's trajectory are salient markers, and an active, spatial representation of both locations is likely formed. Once the target is turned off, induced target motion will stop, and hence estimates of the post-illusory, final target position should be relatively accurate and unbiased (figure 1c). Conversely, since the background motion endures well beyond target onset, so will the illusion. Since the target is continually being perceived as moving diagonally while, concurrently, its current position is perceived relatively accurately and without distortion, it is the spatial, working memory (or active, spatial representation) of the target's initial position that should be distorted online as long as the target remains present, and the illusion sustained. The only way to reconcile the observer's representation of the target's past, initial position both with the subsequently unfolding illusion, and the veridically perceived present position is for the target's initial vertical coordinate to be biased *opposite* the perceived vertical component of the target's trail (figure 1c). Thus, we anticipate that estimates of the target's initial position should be biased in a direction opposite the perceived motion of the target, whereas those of the post-illusory, terminal position should not, even when the stimulus response interval (SRI) for either position is identical.

It is also possible that the observer's representation of the target's initial position is stable, so that the subsequent illusion is unable to change it. Then, by this account, estimates of the target's origin should be unbiased.

Errors were analyzed by computing the mean pointing error across trials. Pointing error on any given trial is defined as the difference, measured in degrees of visual angle, between the target's true location in space and its perceived location, with a positive value signifying mislocalization in the direction of the perceived target motion, and opposite that of the background dots. Thus, pointing error is a measure of the amount of directional bias. In some experiments, we also measure the standard deviation which gives the degree of precision or variability in the data.

Before embarking on the experiments comparing initial and final judgments of position localization in which the confounding influence of SRI is eliminated, we explored the effects of SRI on pointing responses.

2 Experiment 1: Effects of time delay on localization

To characterize the effects of SRI, we designed a task ('time delay task') in which the observer ($n = 5$; two authors, three naïve), after viewing the Duncker illusion, had to estimate the last location of the target just before it was turned off, with or without an intervening 3 s delay between the target offset, and the initiation of the pointing movement. It was expected (Bridgeman et al 1997) that the effect of the illusion should be uncovered under a delay; therefore positional inaccuracy and, more importantly, the bias in position estimates—a signature of the illusion—should be enhanced. Based on our hypothesis, however, since no new perceptual events occurred following the offset of the target, estimates should not be biased any more because of the delay.

2.1 *Methods*

2.1.1 *Stimulus.* All stimuli were presented on a Sony Trinitron monitor (75 Hz refresh) under control of a Mac PowerPC running MATLAB (Mathworks Inc.) and Psychophysics Toolbox (Pelli and Brainard). In our task, a target subtending a diameter of 0.65 deg with a luminance of 54.0 cd m^{-2} underwent real horizontal motion at a velocity of 10.1 deg s^{-1}. The background consisted of a full field of 10 000 randomly placed dots, and thus occupied the entire screen. The mean dot density across the monitor was approximately 2.3 dots deg^{-2}. The dots were both smaller in size (11 min of arc diameter each) and of lower luminance (10.3 cd m^{-2}) than the target. All of the background dots drifted uniformly (100% coherence) at a vertical speed of 8.1 deg s^{-1}. The directions of target motion (leftward/rightward) and background motion (upward/downward) were randomized on every trial. Across trials, the vertical coordinate of the target was randomly chosen from a predetermined range ([28 deg, 32 deg]) below the fixation marker, and the initial horizontal coordinate was 9.5 deg left (right) of the fixation marker when the target drifted right (left).

2.1.2 *Procedure.* Each observer's ($n = 5$) head was partially immobilized by means of a chin-and-head rest placed 28.5 cm from the computer monitor (screen dimensions: 75 deg $\times$ 60 deg). Viewing was binocular. Room lights were turned off (room illumination = 0.01 cd m^{-2}), and the observer had to maintain gaze on a fixation marker, located approximately 1 deg above the screen, throughout the trial. After stimulus offset, and upon hearing a beep, the observer dragged a mouse cursor and clicked the button when the cursor was at the remembered target location. The location of the mouse click was stored along with the true location of the target. The mouse had a resolution of 3.5 min of arc along both axes. There were eight types of trials;

trials were specified by the direction of target motion (left/right), inducer direction (up/down), and SRI (0 s/3 s). There were 20 trials per condition, for a total of 160 ($= 20 \times 8$) trials per observer. Trials for all eight conditions were randomly interleaved.

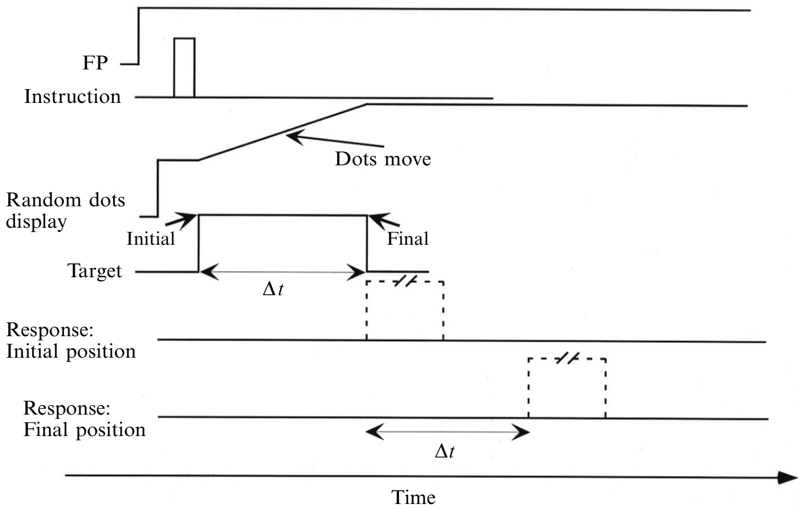
2.2 *Results and discussion*
Interposing a delay did not bias the pointing error more (mean pointing errors for 3 s SRI: 1.3 deg, and 0 s SRI: 1.6 deg; one-way ANOVA: $F_{1,8} = 0.10$, $p > 0.75$), but did marginally decrease the degree of variability (one-way ANOVA: $F_{1,8} = 3.37$, $p = 0.1$). These results are in accord with our hypothesis, but disagree with Bridgeman et al (1997). In fact, the only difference between the conditions in our task—less variability in the 3 s SRI case—can be explained by postulating an increase in unbiased, random noise in spatial memory over time. Thus, delay did not systematically bias estimates of the target's terminal position. Could the illusion systematically bias spatial, working memory of non-terminal target locations?

3 Experiment 2: Systematic errors in localization
To answer this question, we conducted an experiment in which observers had to point to either the initial or final target locations on separate, randomly interleaved trials. On the final position trials, a delay between stimulus (target + background) offset and response was inserted. The delay was equal to the time the target stayed on, and equated the SRI for both positions (Δt in figure 2a). Since there was a blank field at the time of response, the task was a response to an internally stored representation of the target position, not a perceptual one. It has been argued that an immediate motor response is based on sensorimotor input, and uninfluenced by perception, but a delayed one is influenced by perception (Bridgeman et al 1997). If true here, and ignoring the fact there is induced target motion following target onset, but not following offset, equating the SRI should eliminate any differences in estimating the target's initial versus final positions. On the other hand, because of the timing of the illusion relative to the times of the two positions, we predict that the error in localizing the origin should be greater, and biased in a direction opposite the perceived motion of the target.

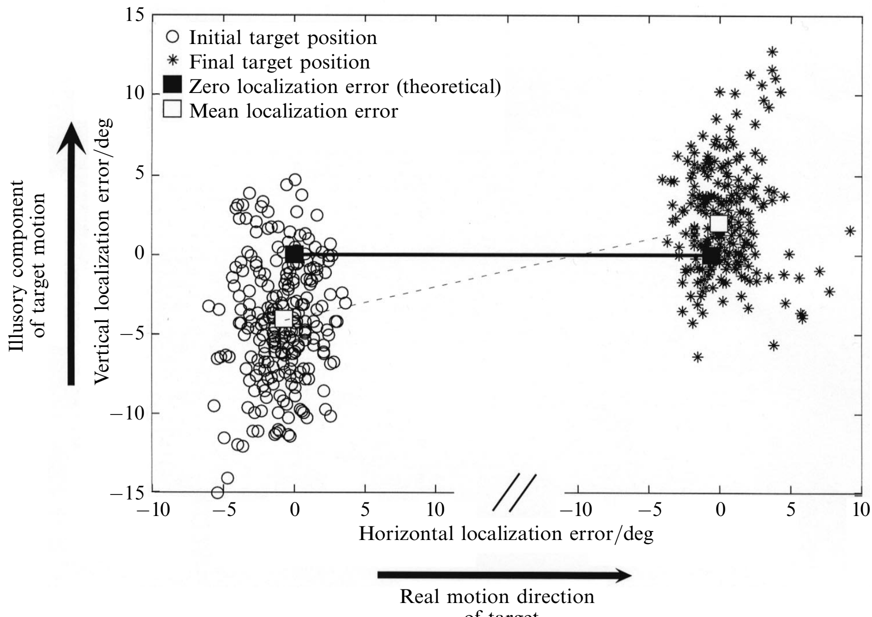
3.1 *Methods*
There were eight types of trials, each trial uniquely specified by the direction of target motion (left/right), the direction (up/down) of the inducer dots, and the target position (initial/final) to be estimated. Figure 2a shows the timeline. Trials (30/condition) were randomly interleaved. See section 2.1 for details.

3.2 *Results and discussion*
Over the group of observers ($n = 7$), we found a highly significant difference in estimates of the initial and final vertical coordinates (mean pointing error: initial position = -4.1 deg, final position = 1.8 deg; one-way ANOVA: $F_{1,12} = 101.6$, $p < 10^{-6}$). As figure 2b shows, the error in localizing the target's starting position was biased in a direction opposite to the target's perceived motion (up and to the right in figure 2b),(1) but the estimated terminal target position was located beyond the true terminal target position, in the direction of the target's perceived trajectory. The offset in the final position can be interpreted as a perceptual phenomenon. Representational momentum (Freyd and Finke 1984), a phenomenon in which the final position of a just offset target is localized beyond its true position in the direction of the perceived trajectory, can explain our data; this effect is interpreted as the result of a perceptual continuation of the motion (Palmer 1999), not a genuine memory effect. Relatedly, Ramachandran

(1) For the same target moving on a blank background or one containing static dots, there was no significant bias of its origin.



(a)



(b)

Figure 2. The delay equalization task timeline and grouped observer data. (a) The fixation marker (FP) was present throughout the experiment. Upon trial onset, a display consisting of a full-field of stationary, randomly placed dots appeared. The observer was informed which target position (initial/final) had to be localized. Next, the target appeared and began moving horizontally. Simultaneously, the dots also began drifting vertically. After time Δt following the target's onset, the target was turned off and background motion concurrently ceased. On initial-position trials, the mouse cursor became visible instantaneously and the observer could respond right away. On final-position trials, there was a delay, equal to the time the target stayed on (Δt), before the mouse cursor was rendered visible. (b) The combined raw data ($n = 7$) are shown. Data across all four conditions [(target motion right/left) × (background motion up/down] are merged. In the graph, the background dots drift down; the target starts out on the left and moves right. The initial-position error (open circles; mean error: −4.1 deg, open square on left) is about twice that of the final-position error (asterisks; mean error: 1.8 deg, open square on right) and in the predicted direction.

and Anstis (1983) showed that an object once seen moving in one direction tends to be perceived as moving in the same direction. This effect shows how motion perception can be biased, and is also a perceptual (not memory-based) effect. Most importantly, the outcomes in experiment 2 confirm our predictions (compare figures 1c and 2c). Since the SRI was identical, only a difference in the relative influence of the illusion can account for the difference in localizing the two positions.

4 Experiment 3: No delay between stimulus and response

It is possible that the long delay (1.9 s) between stimulus presentation and observer response in the previous experiment was long enough to render judgments of target position inaccurate, and may even underlie the enhanced motor bias in estimating the target's initial position. A logical inference from this view would be that motor bias could be eliminated by having observers point as soon as the target passed the required location (whether initial or final). We tested this claim in a new 'no-delay task', in which the observer ($n = 7$) could respond as soon as possible (which was upon target onset on initial-position trials, and upon target offset on terminal-position trials). Therefore, as before, the SRI on the two positions was exactly equal.

4.1 *Methods*

Unlike in experiment 1, the inducer continued to drift in the same direction even after target offset until the observer responded by clicking on the mouse button. Other details are the same as those described in section 2.1.

4.2 *Results and discussion*

Consistent with the results of experiment 1 showing greater accuracy with less delay, the magnitude of the pointing error as compared to that in experiment 2 was diminished (initial position—mean pointing error: -2.6 deg; final position—mean pointing error: 1.3 deg). Note, though, that the error was biased in the same direction, and the difference in error between the two positions was still significant (one-way ANOVA: $F_{1,12} = 37.52$, $p < 0.0001$), as in experiment 2. Thus, the results mirror those in experiment 2 to a considerable degree. In experiment 3 though, since the inducer dots continued to drift even after target offset, the stimulus conditions during the execution of the response were very similar between the two target locations, with the only material difference being that the target was present (and moving) during the response execution in the initial-position trials. Hence, the significantly greater motor bias in the estimates of the initial position could only be explained by the fact that the illusion was continuing to be perceived while the observer pointed to the target's initial location, not while pointing to its terminal location. Note that observers take more than 2 s on average to respond (mouse button click) even on this task.

5 Experiment 4: Varying inducer velocity (the illusion) biases motor estimates of the target's origin, not those of its end point

We have claimed that pointing estimates of the origin in the target's trajectory were biased by the induced motion more so than the estimates of the end point. If so, varying a parameter that is known to modify the illusion should significantly affect pointing estimates of the target's initial position, while localization of the target's final position should remain relatively unchanged. It is known that inducer velocity affects the speed of perceived target motion (Wallach and Becklen 1983). So, we varied inducer (vertical) velocity (2.0 deg s^{-1}, 4.1 deg s^{-1}, 12.2 deg s^{-1}; figure 3a), while keeping the target's true (horizontal) velocity, and target and inducer motion durations the same.

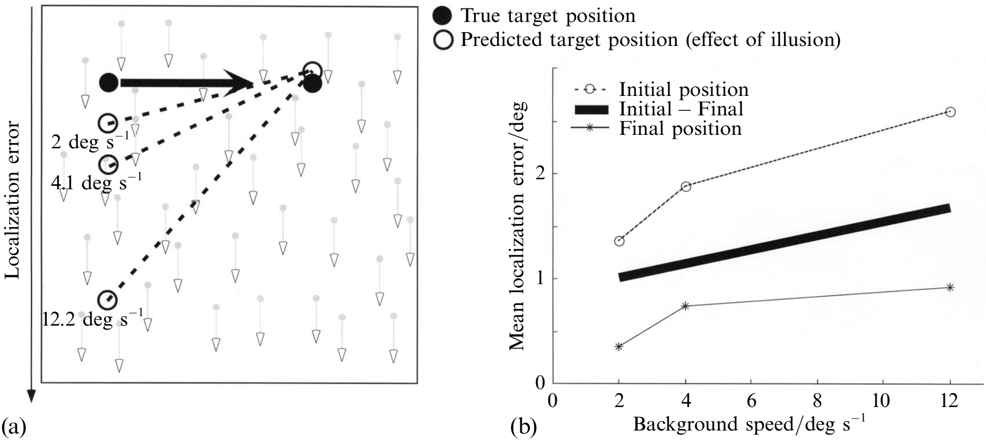


Figure 3. Predicted mislocalizations in the speeds task, and grouped ($n = 4$) data. (a) The target starts on the left and moves right, and the dots drift down. With increasing inducer (vertical) velocity, the bias in the initial-position error should increase (left open circles), whereas the final target position should be unaffected. (b) The effect of inducer velocity on error is shown. The error in localizing the target's initial position (open circles) increased monotonically with inducer velocity, albeit not linearly, whereas the final-position error (asterisks) flattened out. The difference between the two (final – initial) is represented by a thick line.

5.1 *Methods*
See section 3.1 for more details.

5.2 *Results and discussion*
Mean pointing errors ($n = 4$) for the initial position at 2.0 deg s^{-1}, 4.1 deg s^{-1}, and 12.2 deg s^{-1} inducer speeds were −1.4 deg, −1.9 deg, and −2.6 deg, respectively. Corresponding errors for the final position were 0.4 deg, 0.7 deg, and 0.9 deg. In figure 3b the pointing error is plotted versus background speed. The difference in the error between the target's initial and final vertical coordinates varied linearly with inducer velocity (figure 3b: thick line). Indeed, on initial-position trials, inducer velocity (and by inference, the illusion) had a highly significant effect on the pointing behavior (pointing error: t-test, $p < 10^{-6}$), but an insignificant one on the position estimates of the end point (pointing error: t-test, $p > 0.18$). This result shows that the illusion alters spatial, working memory, ie active, spatial representation, of a location the target occupied in the past, but perception of the (post-illusory) present is affected less.

6 Can reconstruction from trajectory explain the error?
It is possible that spatial, working memory about the target's origin is formed, and is then continually being distorted as the target continues to drift. Alternatively, the position could have been retraced back from the target's final point on the basis of memory of its path alone. This view of trajectory-based reconstruction is that there is no direct, stored representation of the target's origin. We conducted a series of experiments, described below, whose results refute the extrapolation (from path) view.

6.1 *Experiment 6a: Random walk in a horizontal direction*
One way to test the no-position-memory view would be to randomize the entire path of the target. In this experiment, the target's vertical coordinate remained unchanged throughout, but the horizontal coordinate was randomly displaced, to the left or to the right, by a constant magnitude from its current position on every time step. Basically, the target executed a random walk in the horizontal direction while the dots flowed upward or downward. Since there was no explicit and definite path, the target's trajectory on any given trial would be nearly impossible to store, and, based on the extrapolation

view, any estimate of the target's origin exclusively extrapolated from the spatial memory of it should be randomly distributed about its true location, or, in the least, the bias should be grossly smeared in noise.

6.1.1 *Methods.* The target's initial horizontal coordinate was in the range [−9.5 deg, 9.5 deg]. The size of the step in the horizontal direction (left/right) was 0.71 deg. Trials were classified according to the direction of inducer motion (up/down). There were 40 trials/condition for each observer. Observers ($n = 4$) had to judge only the location of the target's origin. See section 2.1 for details.

6.1.2 *Results.* Estimates of the target's initial vertical coordinate were biased in the direction opposite the perceived target motion, similar to what was found in previous experiments (mean error = −1.8 deg; *t*-test, $p < 10^{-5}$). Moreover, there was a significant linear correlation between the estimated and actual initial target vertical coordinates ($r = 0.42$, $t_{319} = 7.85$, $p < 10^{-5}$), showing that a positional, working memory of the target's initial location had been created.

6.2 *Experiment 6b: Random walk in a vertical direction*

In another task, complementary to the one above, the target drifted horizontally with uniform velocity on a background in which the inducer dots again moved in a vertical direction. In addition, however, the target was physically displaced randomly up or down by a fixed amount at every step, thereby undergoing a random walk along the vertical dimension. Here too, it would be nearly impossible to keep track of the target's trajectory. Again, observers ($n = 4$) had to estimate the target's initial position only.

6.2.1 *Methods.* The size of the step in the vertical direction (up/down) was 0.59 deg. Trials were classified according to the direction of inducer motion (up/down) × direction of uniform, horizontal target motion (left/right). There were 20 trials/condition for each observer. See section 2.1 for additional details.

6.2.2 *Results.* As in the previous task, we found a significant bias in the judged location of the target's origin. The bias and the perceived motion of the target were in opposite directions, similar to the results of other experiments (mean error = −2.6 deg; *t*-test, $p < 10^{-40}$). Again, there was a significant correlation between the real and judged initial vertical coordinates ($r = 0.44$, $t_{319} = 8.19$, $p < 10^{-5}$).

6.3 *Experiment 6c: Effects of knowledge about the illusion on pointing*

In this experiment, which also aimed to test the relative merits of the online-updating account and the trajectory-based reconstruction account, naïve observers ($n = 4$), who had no prior knowledge of the illusion, had to estimate just the target's initial position in the first session. At the end of the session, we visually demonstrated the illusion by introducing a horizontal reference line in the stimulus which nulled the illusory motion. After being convinced that the target moved only horizontally, the observers ran again. If the observers were extrapolating the target's origin from its final position the first time, later knowledge of the illusion would eliminate the extrapolation, and also the bias in the second session, even though perception of the illusion may not have been affected. Conversely, if the bias were retained to an appreciable degree, it would argue in favor of an updating of spatial, working memory, and against the a posteriori trajectory-based reconstruction view.

6.3.1 *Methods.* See section 2.1 for additional details.

6.3.2 *Results.* As expected, the naïve observers estimated the target's initial vertical coordinate in the opposite direction from its perceived, illusory-motion component (mean pointing error = −3.0 deg; *t*-test, $p < 10^{-14}$). After learning of the illusion, observers did the same task again. Despite being armed with the new knowledge that what they were perceiving was merely an illusion, observers still showed an unequivocal, although somewhat smaller, bias in their estimates of the target's starting position (mean pointing error = -2.1 deg). The bias was still significantly different from zero ($p < 10^{-9}$, t-test).

6.3.3 *Discussion.* Experiments 6a, 6b, and 6c argue against the view that the target's spatial location was simply extrapolated from memory of the trajectory. These results together argue for an account based on an online, automatic updating of spatial, working memory, not trajectory extrapolation.

7 Discussion

We have shown that, for a target undergoing induced motion, estimates of its initial position were significantly biased in a direction opposite that of the target's perceived motion, and were significantly less accurate than those of the target's terminal position, even when the delay between stimulus and response was identical on both positions. The discrepancy in the error between the initial and final target locations reflected the presence/absence respectively of the illusion subsequent to each.

7.1 *Relationship with prior studies*

We analyze previous reports in light of our findings. Brenner and Smeets (1994) and Smeets and Brenner (1995), using a similar motor task as ours, argued that estimates of velocity were influenced by background motion, but estimates of the current target position were not. It may be that velocity estimates were biased by the illusion, whereas position estimates were not. Judgments of velocity are likely to be based on (or at least, correlated with) the perception of past target positions. We have shown that the perception of induced motion subsequent to an event can manipulate a working representation of the event, which may explain their velocity data. In the Bridgeman et al (1979, 1981) studies, observers had to judge the stimulus center (1979), or target position (1981), only after the inducing stimulus had already been displaced, equivalent to our final-position data. Since there was no ongoing illusion during the response, their lack of a perceptual bias is not too surprising. Bridgeman et al's (1997) findings on delay biasing motor response, we believe, reflects a more general biasing of spatial, working memory by subsequent perceptual experience, which, in turn, biases sensorimotor judgment later. We have found (Sheth and Shimojo, submitted) a delay-dependent bias in perceptual judgment, in which no sensorimotor transformations need be computed. In Aglioti et al (1995), the Ebbinghaus illusion was found to affect the perception of object size, but not the grip aperture. However (see their figure 4), the scaling of the grip early on in the reaching movement was affected, because the illusion was perceived at that instant. Later in the movement, the grip aperture scaled according to true disc size, and not the illusion. As our study comparing initial and final position localizations shows, the relative timings of the perception of the illusion and response are crucial. Aglioti et al's grip-aperture result could have arisen because illusory perception of the disc size itself may have later become contextualized by the size of the approaching hand, and therefore corrected.

7.2 *Possible explanations for our findings*

We argue that spatial, working memory of the target's origin was systematically distorted by subsequent perceptual events, and this interaction, in turn, biased motor behavior. This distortion is one of active, working memory, not some revision of a stored value in an otherwise passive memory, nor a memory distortion upon recall that arises as a result of mixing of misleading information and subsequent recommitment to memory, as found in cognitive memory studies (Loftus and Palmer 1974).

There are several other promising accounts for our data which are not based on spatial, working memory. But, as we explain below, none of them suffice to explain the data. Zivotofsky et al (1996, 1998) have studied accuracy of saccades towards a target flashed briefly while a second (primary) target simultaneously underwent induced motion, and have shown that the illusory target motion after the flash of the first target contributes substantially to target mislocalization. They, too, claim their data can be best accounted for by a model in which the illusory stimulus corrupts working memory. Unlike they, we carefully controlled for time delay by equalizing the SRI for initial and final locations. Moreover, we showed that extrapolation of the target's trajectory from its final position could not yield the data, but that it was spatial memory of target position that was being stored, and later distorted on-line, by the illusory target motion. Our results with arm movements, together with Zivotofsky et al's on eye movements, argue strongly for the effect being independent of premotor planning.

Active tracking of target location in which position is constantly updated has been observed (Assad and Maunsell 1995; Pylyshyn and Scholl 1999), although there are key differences between active tracking and spatial, working memory. Active tracking infers the likely present position of the target, and is not a memory of the past. In our experiments, the target starts out from some position, and then moves through space. Therefore, the target's initial position is one the target occupied in the past and is never the target's current position at any instant thereafter. So, pointing to it several seconds after is likely to require spatial, working memory.

Reconstruction of the target's origin based on other sources of knowledge is a possibility. Retracing the trajectory is one possible source; however, experiments 6a, 6b, and 6c show that even when trajectory could not be remembered, the bias in the error persisted. Dead reckoning, or path integration, in which an online accumulation of displacement in the field allows the observer to point back to the starting point, is another possible strategy. Moreover, it can also account for the data from experiment 6. Path integration, however, is dependent on internal self-movement cues, or efferent copy of motor commands. In our tasks, observers gazed on a stationary fixation marker throughout, and hence no motor commands were generated in the first place. Moreover, path integration itself is overwhelmingly accepted (Israel et al 1997; Takei et al 1997; Gaffan 1998; Maaswinkel et al 1999, to cite a few) as being based on spatial, working memory. Another example of reconstruction would be the moving field inducing a shift in the location of the frame surrounding the moving dots. When the subjects are required to point to the target in the context of the shifted display frame, pointing is shifted in the opposite direction. However, our experiments were conducted in the dark, so the surround frame was hardly visible. Moreover, pointing too was in the dark in most experiments and a shift in the frame, if any, could barely persist to affect pointing under such conditions. Hence, this explanation is somewhat unlikely.

Therefore, our results are consistent with the notion of a *single* variable—spatial, working memory—that simultaneously affects sensorimotor and perceptual maps. To conclude, our findings argue for a close nexus between sensory processes and low-level spatial, working memory.

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