Backward position shift in apparent motion

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We investigated the perceived position of visual targets in apparent motion. A disc moved horizontally through three positions from −10° to +10° in the far periphery (20° above fixation), generating a compelling impression of apparent motion. In the first experiment, observers compared the position of the middle of the three discs to a subsequently presented reference. Unexpectedly, observers judged its position to be shifted backward, in the direction opposite that of the motion. We then tested the middle disc in sequences of 3, 5, and 7 discs, each covering the same spatial and temporal extents (similar speeds). The backwards shift was only found for the three-disc sequence. With the extra discs approaching more continuous motion, the perceived shift was in the same direction as the apparent motion. Finally, using a localization task with constant static references, we measured the position shifts of all the disc locations for two-disc, three-disc and four-disc apparent motion sequences. The backward shift was found for the second location of all sequences. We suggest that the backward shift of the second element along an apparent motion path is due to an attraction effect induced by the initial point of the motion.

Introduction

Many studies have reported that motion can shift the perceived location of an object: Fröhlich (1930) first observed that when an object appears abruptly and moves, the initial position of the object is seen to be displaced ahead of the actual starting point; in the flash-lag effect (MacKay, 1958; Nijhawan, 1994) a moving object appears to lead a static flash when they are physically aligned; the moving texture embedded in a static aperture biases the perceived position of the aperture (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990); when a transient feature change is imposed on a moving object, the position of the feature change is mislocalized to a later point (Cai & Schlag, 2001). Whitney and Cavanagh (2000) further demonstrated that a flash is dragged by a spatially remote moving texture even though it does not contain a motion signal itself (Cavanagh & Anstis, 2013). This flash-drag effect has been found in different variations including higher-order motion (Shim & Cavanagh, 2004; Watanabe, Sato, & Shimojo, 2003) and attentive tracking (Shim & Cavanagh, 2005; Tse et al., 2011). One common characteristic of this motion-induced position shift is that the position of an object is shifted forward in the direction of the motion. Researchers have proposed that this extrapolation might compensate for the effects of the inevitable neural delays in computing the position of a moving object (see Whitney, 2002, for a review; but also see Eagleman & Sejnowski, 2007).

Here we report an unexpected effect, a backward position shift, where a moving object is shifted in the direction *opposite* to that of the motion, toward the initial point of the motion trajectory. This effect is different from the repulsion effects reported earlier on the onset (Thornton, 2002) or the offset (Müsseler, Stork, & Kerzel, 2002) position of a moving target. The backward shift here is found on the intermediate positions along the motion path.

In our first experiment, we presented three discs (the initial disc, the target, and the trailing disc) sequentially along a horizontal trajectory at 20° eccentricity (Figure 1 and Movie 1). When asked to judge the position of the middle disc, surprisingly, observers mislocalized the

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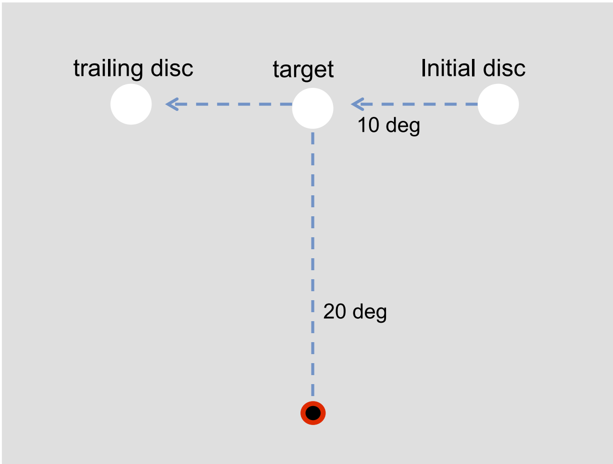


Figure 1. Example of the stimuli used in Experiment 1. Here a leftward motion direction condition is shown. Three-disc apparent motion was presented 20° above the fixation point. The target is the middle disc aligned with the fixation. The initial disc and the trailing disc were both separated by 10° from the target.

middle disc closer to the initial disc, in the direction opposite to that of the motion. We then showed that this backward shift of the midpoint of the apparent motion is diminished and turned into forward shift when the apparent motion has more steps (becomes more continuous). Finally, we analyzed the position shifts seen at each location when two-, three-, and four-disc apparent motion were presented. We find a Frölich effect at the first location, a backward step at the second location that grows larger as the number of steps increases, and a shift at the third location that changes from little effect to a large shift in the direction of motion. We attribute these effects to position attraction of intermediate locations toward the beginning and end locations of the apparent motion sequence.

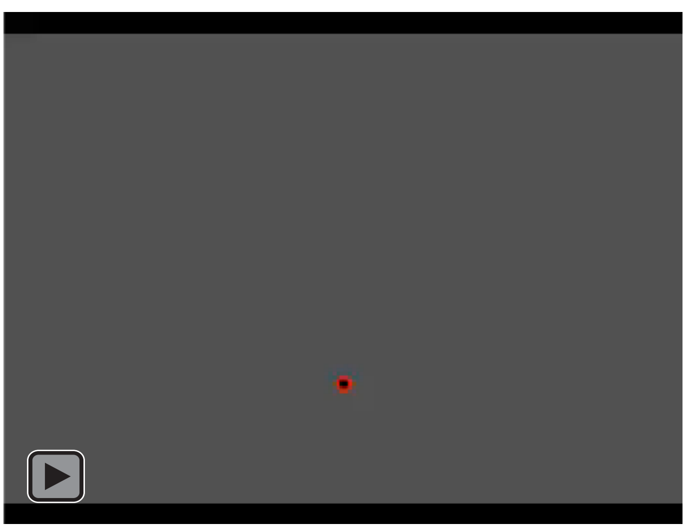
Experiment 1

In this experiment, we evaluated the perceived position of the central stimulus in a three- stimuli sequence (Figure 1). This display created a strong impression of apparent motion across the three locations, but observers could still see the three discrete disc locations along the motion path. We had separate conditions with the central target the same color (Movie 1) as the first and last disc (white) and with the central target green (Movie 2), to distinguish it from the first and last. The unique color is not necessary here as subjects can easily isolate the location of the central target when there are only three discs. However, we wanted to test whether the results would be affected by the unique target color as we will need to use this color cue in later experiments to help subjects isolate the target when there are more than three discs.

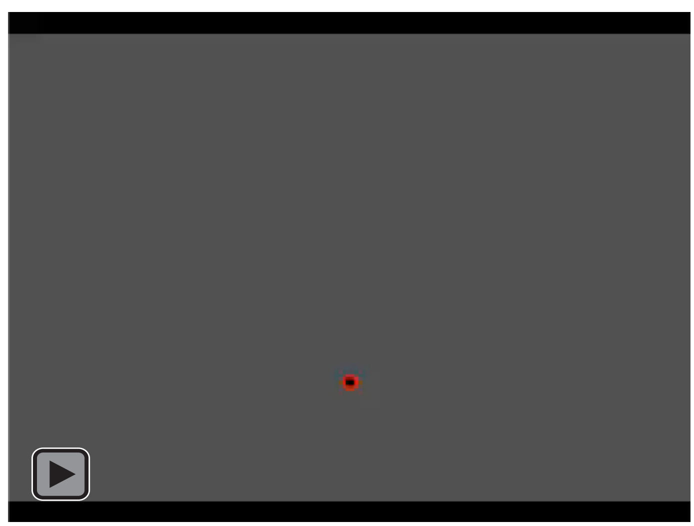
Method

Observers

Twelve observers (one of the authors and eleven naïve observers recruited from Dartmouth campus, age 19–27) with normal or corrected-to-normal vision participated in the experiment. Written, informed consent was obtained from each observer before the experiment.



Movie 1. Demonstration of the three-disc apparent motion with white central target used in Experiment 1.



Movie 2. Demonstration of the three-disc apparent motion with green central target used in Experiment 1.

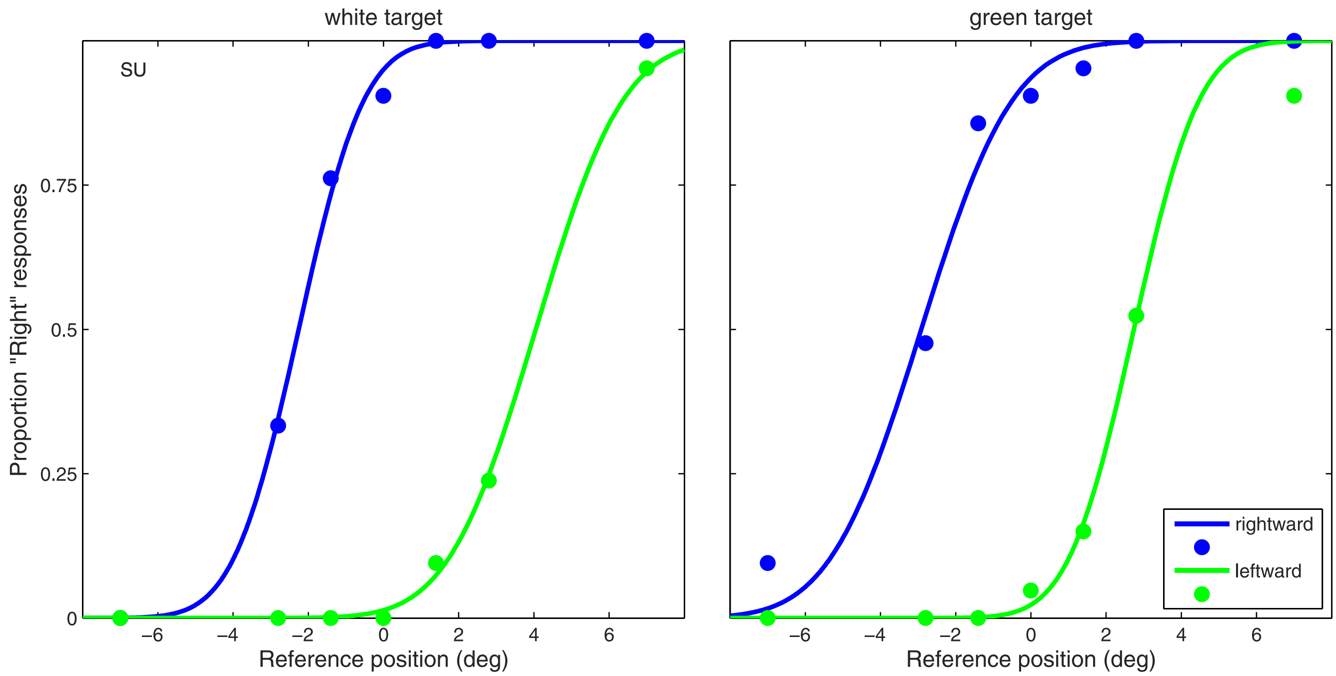


Figure 2. Psychometric functions from one representative observer for two motion directions (leftward and rightward) and two target colors (white and green). PSEs in Figure 3 were based on data pooled across both colors and directions (see Methods) as the results did not differ for either of these two factors.

Stimuli

The observers were tested in a dimly lit room with a chin rest 37 cm away from a 17-in. Mitsubishi CRT monitor (800 × 600; 60 Hz). We used a PC with Psychtoolbox (Brainard, 1997; Kleiner et al., 2007) run on MATLAB for experimental control and stimulus generation.

The fixation point was a 0.3° diameter black bull's-eye with red outline located at 10° below the center of the monitor. The three-disc apparent motion (Figure 1) was composed of three discs, the initial disc, the target, and the trailing disc, presented sequentially on a gray background (50 cd/m^2). The initial and trailing discs were always white (101 cd/m^2) but the target disc was either white (also 101 cd/m^2) or green (86 cd/m^2). Each disc was presented for 50 ms with 50 ms interstimulus interval (ISI) between their presentations. All the discs had a width of 2.5°. The target was always presented 20° above the fixation point. The initial disc and the trailing disc were 10° horizontally left and right of the target.

Procedure

Each trial started with the presentation of the fixation point. Observers were required to maintain their fixation throughout the entire experimental session. After a random delay between 500 and 600 ms, the three-disc apparent motion sequence was presented. The direction of the apparent motion was either rightward or leftward, randomly interleaved across trials. After the offset of the trailing disc, and a random interval between 400 and 500 ms, a vertical black bar (3.5° × 0.3°) was presented on the apparent motion path as a reference. The observers' task was to report whether the target was right or left of the reference. The reference was presented randomly at one of seven horizontal positions (from −7° to 7° relative to the target; a narrower range was used for some observers). The target color was either green or white, in separate blocks. There were 42 trials in each block, and blocks with different target colors were randomly interleaved.

Results

We initially fit cumulative Gaussian functions to the four psychometric functions (the four combinations of left vs. rightward motion and green or white targets) for each observer using constrained nonlinear optimization functions in MATLAB. The psychometric functions obtained from one representative observer are shown in Figure 2.

The reference position at which observers judged the target as right of the reference at 50% probability was taken as the point of subjective equality (PSE), and it was used to estimate observers' perceived position of the target. The magnitudes of position shifts were unaffected by the direction of motion, repeated-measures analysis of variance (ANOVA): $F(1, 11) = 2.36$, $p = 0.153$,or the color, repeated measures ANOVA: $F(1, 11) = 4.64$, $p =$

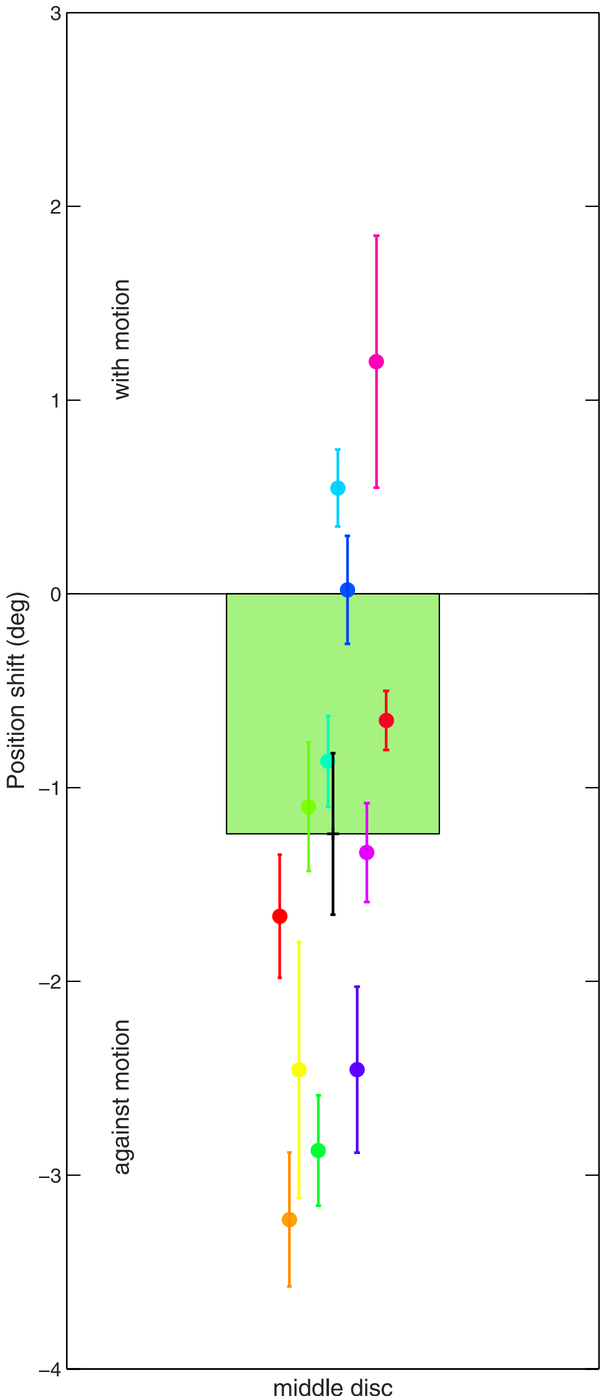


Figure 3. Position shift of the middle target disc induced by the apparent motion across the three discs. Observers' perceived positions of the target were estimated by PSEs derived from their individual psychometric functions. Data from two motion directions and two colors were pooled. The positive values here represent the position shift in the direction of motion, and the negative values represent the shift in the direction opposite to that of the motion. The results of Experiment 1 revealed a backward position shift: Targets are seen shifted against the direction of the apparent motion. The error bar of the group mean represents ±1 *SEM*. Individual PSEs are plotted as differently colored dots, and the error bars are the standard errors of the individual bootstrapped PSEs.

0.054, of the target, so we pooled the data from both directions and both target colors to generate one psychometric function for each observer. After the pooling, each data point on each observer's psychometric function represented at least 96 measurements. We tested white and green targets here to see if the results would be affected by the two different colors we used. They were not. In the later experiments, we used only the green targets in order to make the target more distinctive from the other discs when the apparent motion sequences consist of more steps.

The PSE averaged across observers is depicted in Figure 3. The target's perceived position was shifted backward, in the direction opposite to that of the motion, $t(10) = -3.10$, $p = 0.010$. Individual PSEs are also shown in Figure 3 along with their standard deviations estimated with a bootstrap procedure (each observer's original data was resampled and the psychometric functions were fitted 1000 times).

For each observer, we used the 0.1th and 99.9th percentiles of the bootstrapped PSEs as the criteria, and tested whether the distribution of each observers' bootstrapped PSEs significantly deviates from zero. At the individual level, nine out of twelve observers showed significant ($ps < 0.001$) backward shifts. Two observers estimated the target location significantly in the direction of motion.

In a separate pilot, we had tested an alternative procedure where observers were asked to use the fixation point as the reference. The position of the second disc was changed across trials, and observers reported whether the target disc was left or right of the vertical (through fixation) to obtain the psychometric functions. The results were the same as here. However, physically shifting the target position changes the speed of apparent motion, and the target would be less visible when closer to the neighboring discs. Because of these confounding factors, we chose the comparison of the fixed target location to a variable reference reported above rather than this alternative procedure.

Experiment 2

The backward shift in Experiment 1 is unexpected given that forward extrapolation is reported in many prior studies (see Whitney, 2002; Eagleman & Sejnowski, 2007 for reviews) with only a few exceptions (Thornton, 2002; Müsseler et al., 2002). One characteristic of the apparent motion stimuli that we used is that we presented only three discrete locations on the motion path far in the periphery (20° degree). In the majority of previous studies, the motion was continuous (within the constraints of monitor refresh rates). In Experiment 2, we tested whether the backward shift of

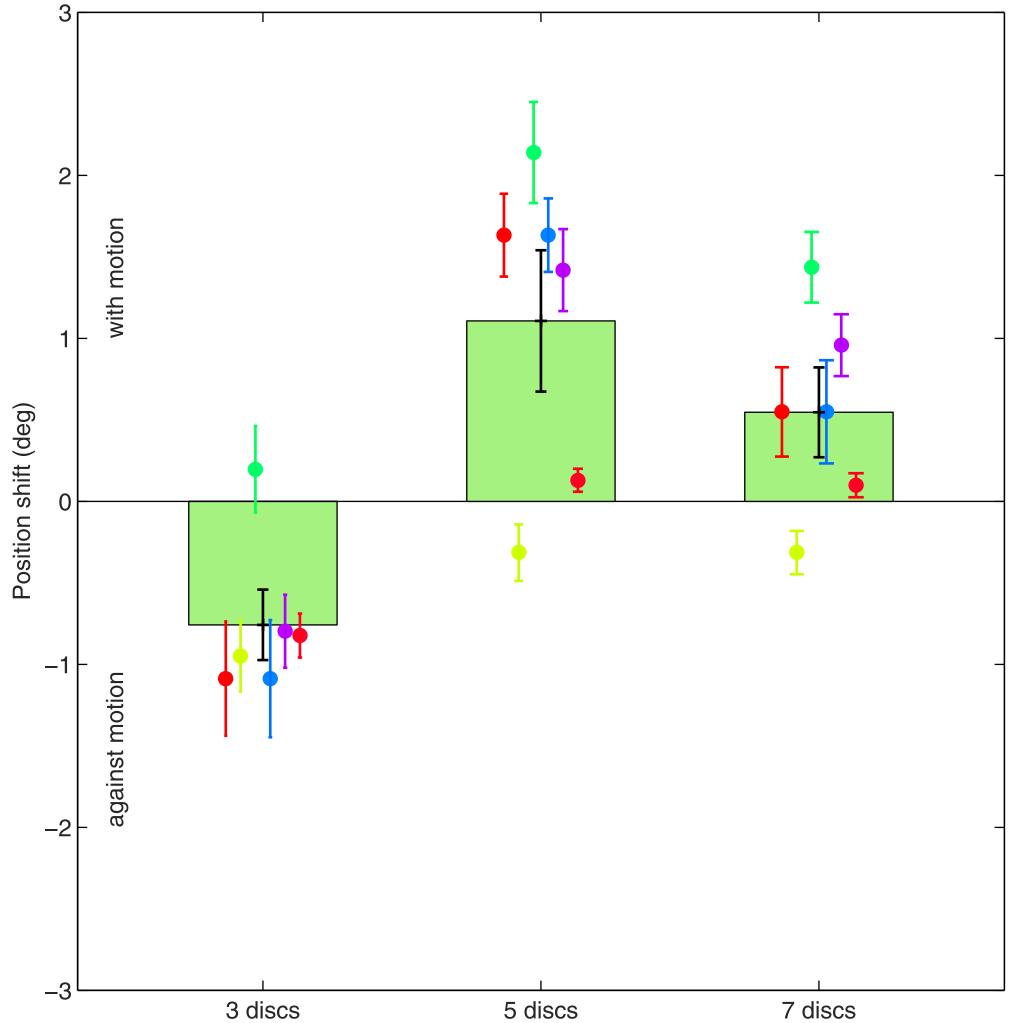


Figure 4. Position shift of the midpoint of continuous apparent motion. Perceived positions of the midpoint of the apparent motion were shifted toward the direction of motion when the apparent motions were more continuous. The error bar of the group mean represents ±1 *SEM*. Individual PSEs are depicted in dots, and the error bars are the standard errors of the bootstrapped PSEs.

the midpoint of an apparent motion path changes when we increase the number of samples along the apparent motion path, keeping speed and duration approximately constant over the path.

Method

Observers

Five observers (one of the authors and four naïve observers recruited from Dartmouth campus, age 20–27) with normal or corrected-to-normal vision participated in the experiment. Written, informed consent was obtained from each observer before the experiment.

Stimuli and procedure

The design was the same as in Experiment 1, with the following exceptions. We used a MacBook Pro with Intel HD Graphics 4000 video card to run the experiment to achieve a higher refreshing rate (100 Hz) of the monitor (17-in. Mitsubishi CRT monitor) required in this experiment. Three conditions were tested in separate blocks: three-disc, five-disc, and seven-disc apparent motion. In all three conditions, the discs were spaced uniformly along the 20° apparent motion path. The target was always the middle disc located 20° above fixation. The temporal structures of the stimuli were the same for all three conditions: The durations of each disc were 50, 30 and 20 ms in three-disc, five-disc and seven-disc conditions respectively. The ISIs between discs were the same as the durations of the discs. The target was always colored green because without any marker, it was difficult or impossible for observers to localize the target disc when there were more than three discs. In addition, the width of the target was increased by 20% compared to the other discs to increase the visibility of the target. The three conditions (3, 5, and 7 discs) were blocked and randomly interleaved within one experimental session.

Results

The results from five observers are presented in Figure 4. The effect of number of steps on the position shift is significant, repeated-measures ANOVA: $F(1, 5) = 26.8$, $p = 0.004$. For all of the observers, the backward shift of the target was found only in the three-disc apparent motion, $t(4) = -3.09$, $p = 0.037$, whereas the targets were shifted forward in the five-disc, $t(4) = 3.09$, $p = 0.037$, and seven-disc, $t(4) = 3.84$, $p = 0.018$, conditions. Thus, the data suggests that when the speed and path length of the motion were held constant, the backward shift of the midpoint changed to a forward shift when the motion path was more densely sampled. We did not add any further samples to better simulate continuous motion, because already with just five samples, the perceived position shift had switched to the same as the motion direction, as reported in previous studies with more continuous motion (Cai & Schlag, 2001; Müsseler et al., 2002; Eagleman & Sejnowski, 2007).

Experiment 3

In Experiment 2, we found a backward shift on the middle disc of the three-disc apparent motion that switched to a forward shift when more steps were added to the apparent motion sequence. When we added the extra steps in Experiment 2, we reduced the step size and the time intervals between steps to keep the speed and distance covered the same. We do not know if the changes seen in Experiment 2 are the result of the smaller steps in space and time or if they generalize to all step sizes. We also do not know if all locations show similar position shifts or if they are confined to the central location. To address these questions, we measured the position shifts of all the steps along the apparent motion paths with two, three, and four discs in the sequence and we kept the step size and timing fixed as more elements were added.

In addition, an earlier study investigating the onset repulsion effect (Kerzel & Gegenfurtner, 2004) suggested that the motion-induced position shift is sensitive to the modality of observers' responses, as they found a reverse shift when evaluated with a motor response but a forward shift when evaluated with a perceptual judgment. We therefore asked observers in our new experiment to report target by clicking on the remembered screen location. We found that the backward shift observed in Experiment 1 and Experiment 2 was also found in the corresponding conditions here even though the task involved a motor response (mouse click to remembered location) rather than a perceptual judgment.

Method

Observers

Seventeen observers (one of the authors and sixteen naïve observers recruited from Dartmouth campus, age 19–27) with normal or corrected-to-normal vision participated in the experiment. Written, informed consent was obtained from each observer before the experiment.

Stimuli and procedure

The target to be reported in each sequence was colored green to distinguish it from the white non-targets. Observers reported perceived target location by moving a cursor on the screen and clicking at the remembered location. A series of static tick marks ($3° \times 0.27°$) were used as the reference, and were presented above the apparent motion path.

The stimuli were presented at 20° above the fixation. The horizontal distances between neighboring discs were 10° in all apparent motion stimuli used here, and the midpoint of the motion path was aligned with the fixation. Thus, the only target presented right above the fixation point was the second disc of the three-disc apparent motion. The duration of each disc and the ISI between discs were the same as the parameters used in Experiment 1. Fifteen line segments (spanning horizontally from $-21°$ to 21° and centered vertically 3° above the apparent motion path) were used as the reference. These tick marks were presented on the screen throughout the whole experimental session. At the beginning of each block, an instruction was presented on the screen to inform observers how many discs there were in the apparent motion stimuli, and which disc was the target in that block. Observers were asked to localize only one disc in each trial. Each trial started with the onset of the fixation point. The fixation point blinked for 300 ms, reminding observers to maintain their fixation. After a random interval between 400 to 500 ms, in which the fixation point stayed static, the apparent motion stimuli were presented. After the offset of the last disc, and a 300 ms interval, a horizontal line spanning the entire screen horizontally was presented on the apparent motion path, and the observers moved the cursor to click on the line to localize the position of the target. Nine types of targets, for each of the two-, three-, and four-disc apparent motion conditions, were tested in separate blocks. Two motion directions were mixed within a

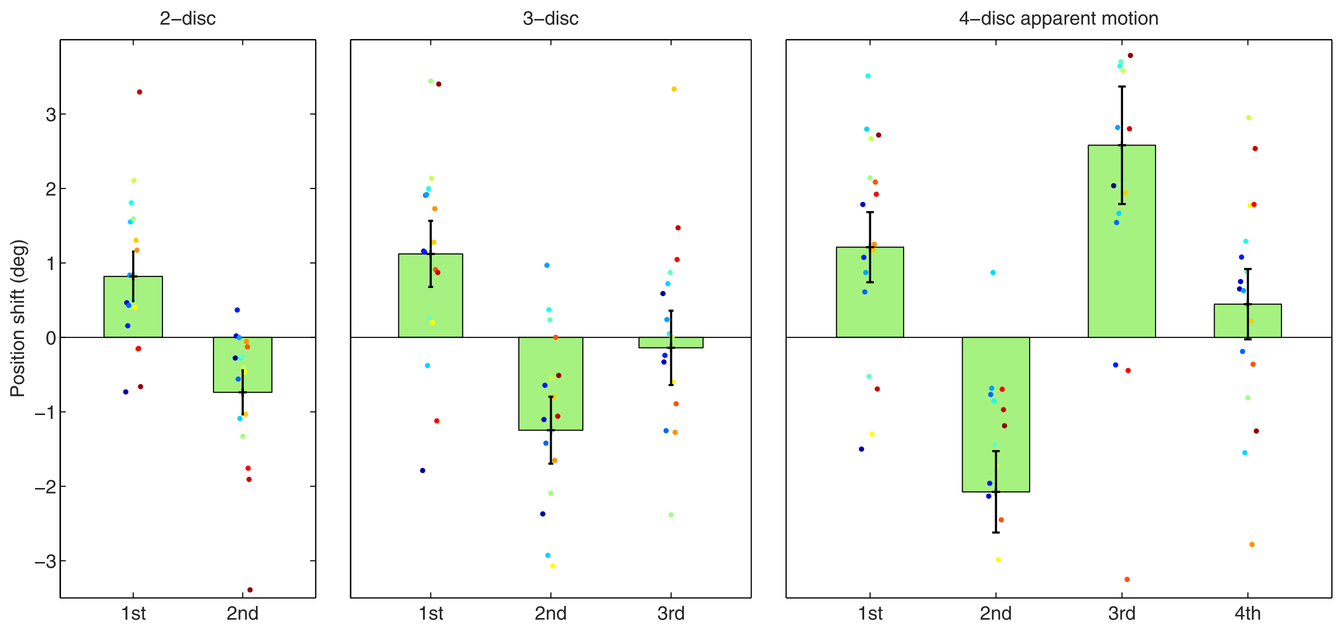


Figure 5. Position shifts of all the steps along the two, three, and four-disc apparent motion paths. Individual data were depicted in dots, representing observers' responses in the localization task. Group error bars are ±1*SEM*.

block. Observer localized each type of targets at least 25 times per motion direction.

Results

Perceived positions estimated in the localization task are plotted in Figure 5. All the tests of the nine a priori hypotheses were evaluated against the Bonferroni adjusted alpha level of 0.006 per test (.05/9) for significance. In the two-disc apparent motion, the perceived position of the first disc was shifted forward, $t(16) = 3.21$, $p = 0.006$, and the second disc was shifted backward, $t(16) = -3.25$, $p = 0.005$.

In the three-disc apparent motion, the position shift differed across the three target positions, repeated measures ANOVA: $F(2, 32) = 10.5$, $p = 0.003$. The first disc was shifted forward, $t(16) = 3.30$, $p = 0.005$, replicating the classic Fröhlich effect. Consistent with Experiment 1 and 2, the second disc of the three-disc apparent motion was shifted backward, closer to the initial point of the motion, $t(16) = -3.61$, $p = 0.002$. However, the termination point of the three-disc apparent motion was not significantly mislocalized, $t(16) = -0.37$, $p = 0.719$.

Finally, in the four-disc apparent motion, the targets shifted by different amounts at each location, repeated-measures ANOVA: $F(3, 48) = 18.3$, $p < 0.001$. The initial point of the four-disc apparent motion was again shifted forward, $t(16) = 3.36$, $p = 0.004$, and the two intermediate discs were shifted in different directions: As was the case in the 2- and 3-disc sequences, the second disc was again shifted backward, in the direction opposite to that of the motion, $t(16) = -4.95$, $p < 0.001$, whereas the third disc was strongly shifted forward, in the direction of the motion, $t(16) = 4.26$, $p < 0.001$. The last disc was not significantly shifted, $t(16) = 1.23$, $p = 0.23$.

The results show that the discs following the initial point were not all shifted backward. The backward shift was only found in the second disc of the apparent motion, and this shift increased as the number of discs in the apparent motion sequence increased. When there were four discs in the apparent motion, the position shift changed from backward at the second location to forward at the third.

Discussion

Across our experiments, we found that the second disc in two-, three-, and four-disc apparent motion was shifted in the direction opposite to that of the motion. The perceived location for the central disc in three-, five-, and seven-disc sequences only shifted backwards in the three-disc sequence (where it was the second in the sequence) but moved forward, in the direction of the motion, for the five- and seven-disc sequences (where it was the third and fourth in the sequence). Our last experiment confirmed that the backward shift was found only for the second item in two-, three-, and four-disc apparent motion sequences.

We suggest that this backward shift occurs because the salient initial disc attracts the second disc towards it (Zimmermann, Fink, & Cavanagh, 2013; Yamada, Kawabe, & Miura, 2008). Although some studies using static stimuli show that a salient stimulus repels the perceived position of a subsequent target (Suzuki & Cavanagh, 1997; DiGiacomo, & Pratt, 2012) others instead report attraction (Zimmermann, Fink, & Cavanagh, 2013; Yamada, Kawabe, & Miura, 2008). Yamada et al. (2011) showed that observers mislocalized a target closer to a salient inducer that preceded it. These authors suggested that the attraction was caused by the averaging of the memorized locations of the target and the precue. According to the authors, this averaging took some time to complete, so they found the attraction effect only when the comparison reference was presented at longer intervals after the target. In contrast, if position averaging plays a role in our experiments, it must not require these longer delays as our references were presented with short (Experiment 1) or no (Experiment 3) delays. Zimmerman et al. (2013) also reported an attraction effect where an initial salient stimulus attracted a subsequent, masked target. These authors also suggested an averaging of location produced by summing the response distributions of the two stimuli. The distribution of the second stimulus is broader as it has less certainty (because of the mask), and so its peak in the summed response distribution shifts more. In our experiments, we did not have a mask, but we might consider the following stimuli in the three- and four-disc sequences as masking the second location. We therefore speculate that the first stimulus in a motion sequence is the most salient and serves to attract only the second, less salient, stimulus.

Previous studies on the motion-induced position shift that used apparent motion did not report a backward shift. Shim and Cavanagh (2004) used a bistable quartet to induce apparent motion, and reported that the flashes presented close to the motion path were shifted in the direction of the perceived motion. The stimuli and the procedure of their study are different from ours in two key respects. First, in their study, the temporal interval between subsequent stimuli was longer (ISI of 195 ms rather than our 50 ms), and the apparent motion stimuli were presented closer to the fixation (5.5°) compared to the 20° eccentricity used here. The backward shift may only occur when the object jumps in large discrete steps (10° horizontal move with 100 ms SOA) in the periphery. Second, while Shim and Cavanagh's (2004) observers were required to attentively track the motion for several cycles before the onset of the test flash, in our experiments, the stimuli were presented only once in each trial, and the directions of the motion were randomly mixed within a block. Shim and Cavanagh's (2004) design may have reduced the salience of the initial stimulus in the apparent motion sequence and increased the salience of the central test flash. In the supplementary demonstration movies (see Supplementary Materials), we added additional fixation points to the central one used in the experiments for readers to experience the effect of eccentricity and motion direction (toward fovea, foveopetal, vs. away fovea, foveofugal) on the position shift. As with many motion-induced position shift effects, the effect disappears when fixating closer to or directly at the target (Whitney & Cavanagh, 2000; Kanai, Sheth, & Shimojo, 2004). We also observed some individual differences for the effect of motion toward or away from the fovea. The flash-lag effect (Mateeff & Hohnsbein, 1988) and flash-drag effect (Shi & Nijhawan, 2008) are significantly influenced by motion direction, and further research may show that this is also the case for the backwards shift we report here.

Our attraction account is speculative at this stage, but it does explain many aspects of our results including the forward shift seen for the third stimulus in the four-disc sequence in Experiment 3 (Figure 5). In this configuration, the final disc is again salient as there are no further stimuli. The third disc would be shifted toward this terminal location, producing a shift in the direction of motion in this case. The displacements of the second disc are also in line with variations of salience and their effect on attraction. Specifically, the second disc was shifted backward by the smallest amount in the two-disc apparent motion and by the largest in the four-disc apparent motion (Figure 5, left vs. right panels). In the two-disc apparent motion, the second disc itself was also the termination point of motion, and so it would also be salient on its own, increasing its spatial certainty and reducing the attraction from the previous, initial stimulus. In addition, this second and last disc of the two-disc sequence is the motion offset, and may be interpreted as a stop or stationary point, again reducing the attraction of the first disc on the second one. However, when the second disc was more remote from the termination location (in three and four-disc sequences), it was less salient on its own and therefore more attracted to the initial stimulus. Thus, the backward shift of the second disc increased from the two- to the four-disc sequences in tandem with this decrease in its salience. Future experiments would need to directly test this speculation as other features also changed with the number of steps in the apparent motion sequence, for example the eccentricity of the second stimulus.

The backward position shift reported here could share mechanisms with the feature integration effects seen for moving stimuli: For example, in Breitmeyer, Herzog, & Ogmen (2008), the change of the directions of the Vernier offset stimuli in two successive frames was underestimated by the observers, as if their values had been averaged. Similarly, Kawabe (2008) reported that the perceived size of a disc is influenced by the size of a disc presented before it, suggesting the sizes feature of the two stimuli had been integrated. With this integration account, the position of an object would be regarded as another visual feature like object size or Vernier offset, and may be integrated across frames. However, it should be noted that the feature integration is not always observed when the features of the stimuli are continuously updated. For example, Sheth, Nijhawan, & Shimojo (2000) reported that when the color of a disc is changed continuously, observers' perceived colors are extrapolated rather than integrated. More importantly, the feature integration account will predict the same direction of position shifts for all the discs along the motion path, a pattern that we did not see. In particular, the third disc shifted away from and not toward the second disc in our four-disc sequence. It is possible that motion perception is built up gradually after the motion onset (Kanai, Sheth, & Shimojo, 2007; Hidaka, Nagai, & Gyoba 2009), and thus, the positions are integrated at the earlier segment of the motion path, and with the maturation of motion perception, the predictive mechanism dominates and the position extrapolation is observed. Further studies will be required to differentiate between our attraction and salience proposal and other alternatives such as integration.

Why have previous studies reported forward motion extrapolation and not a backward shift in tests of motion's effect on perceived positions? We attribute these findings of forward shifts to the use of more densely sampled or continuous motion sequences. In continuous motion, the saliency of the motion onset is diminished by masking (motion deblurring, Burr, 1980) reducing the ability of the onset location to attract subsequent locations. Moreover, our finding suggests that only the immediately adjacent location is attracted toward the first, and with more densely sampled sequences, this distance is already very small and any attraction would be hard to discern. It may be that the backward shift is constrained to high-speed apparent motion that moves in large steps in the periphery.

Keywords: apparent motion, position, mislocalization

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