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Bi-directional illusory position shifts toward the end point of apparent motion

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Abstract

In this study, we examined the relation between motion induced position shifts and the position shifts caused by saccades. When a stimulus is flashed briefly around the time of a saccade, its perceived position is mislocalized toward the saccade target: if the flash is in front of the saccade the test flash appears shifted in the direction of eye movement; but a test flashed beyond the saccade target is displaced *back* toward the saccade target (bi-directional saccadic compression: Ross, J., Morrone, M. C., & Burr, D. C. (1997). Compression of visual space before saccades. *Nature, 386*, 598–601. Motion induced position shifts (in the absence of eye movements) have been demonstrated for a variety of stimuli but the illusory position shift is always found to be in the same direction as the motion. However, all previous studies presented the tests either along or beside the motion path, never beyond its end point. We now test this region beyond the motion path and find that the apparent location of a test in this region is shifted in the direction opposite to the motion, back toward the motion end point. In contrast, when the flash was presented between the beginning and end of the motion path, it is shifted in the direction of motion, again, toward the motion end point. These shifts together indicate a compression of perceived locations toward the end point of the apparent motion. Control experiments confirmed that this effect was neither due to the *Fröhlich* effect induced by apparent motion from the test flash to the second disc nor to foveal compression. The correspondence between compression toward the end point of apparent motion and saccadic compression toward the saccade target suggests that attentional shifts or planned eye movement signals may play a role in both.
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1. Introduction

Recent findings have shown that perceived spatial position is not based solely on retinotopic mapping and can be distorted by other factors. One striking example is saccade-induced mislocalization: a test object briefly presented at the time of eye movement appears shifted from its veridical location in the direction of the saccade (Cai, Pouget, Schlag-Rey, & Schlag, 1997; Dassonville, Schlag, & Schlag-Rey, 1992; Honda, 1989; Matin & Pearce, 1965; Schlag & Schlag-Rey, 1995; see Ross, Morrone, Goldberg, & Burr,

2001; Schlag & Schlag-Rey, 2002 for reviews). These findings were taken to indicate that the perceived location of an object is determined by a combination of the object's retinal position and 'corollary discharge' or 'efference copy' by eye movement signals (see Sperry, 1950; von Helmholtz, 1962). This combination was assumed to compensate for the translation of images on the retina caused by eye movement.

However, it has recently been demonstrated that such mislocalization effects are not uniform throughout the visual field. Rather, the magnitude and direction of localization errors depend on their position in the visual field. When a spatial structure is flashed just prior to a saccade, its location appeared to be closer to the saccade target than it actually was, regardless of whether they were lying in

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front of or behind the saccade target (bi-directional saccadic compression: Lappe, Awater, & Krekelberg, 2000; Morrone, Ross, & Burr, 1997; Ross, Morrone, & Burr, 1997). This is incompatible with the simplistic explanation that a uniform correction would cancel out retinal translation by eye movement signals.

Motion can also affect perceived position in the absence of eye movements and, in general, the perceived position of a brief test appears displaced in the direction of the motion. For example, the starting point of an object's motion is seen farther ahead along the path of motion than its actual location as is the position of an abrupt change in its shape or color while it is moving (Cai & Schlag, 2001; Fröhlich, 1923). The position of a stationary envelope filled with a moving texture is seen shifted in the direction of motion and even a stationary stimulus briefly presented adjacent to a moving stimulus is mislocalized in the direction of motion (DeValois and DeValois, 1991; Ramachandran and Anstis, 1990; Whitney and Cavanagh, 2000; see Krekelberg and Lappe, 2001; Nijhawan, 2002; Whitney, 2002 for reviews).

Whereas there are many studies investigating the effect of motion on position, relatively little is known about whether these effects are uniform through the visual field. In particular, none of the previous studies on motion-induced position distortion tested the mislocalization effect beyond the terminal point of motion, which is perhaps the most interesting location given the saccadic compression effect. Tests presented beyond the saccade target show a backward shift toward the target. In contrast, all motion induced position distortions have been in the same direction as the motion but these effects have only been tested along or near the motion path, never beyond its end point.

The main purpose of this paper is to test whether the direction of the mislocalization effect is uniform regardless of the probed location or whether the mislocalization reverses direction beyond the end point of the apparent motion as is the case in eye movement. To examine this question we test localization of the flash beyond the end point of apparent motion as well as in front of it.

2. Experiment 1

The main purpose of the first experiment was to examine position shifts beyond the end point of apparent motion. We asked observers to localize a brief flash that was presented in the far field of apparent motion with respect to the reference bar, all while apparent motion was being displayed. The test flash was set to occur at various times between the offset of the first disc and the onset of the second disc of apparent motion.

2.1. Method

2.1.1. Observers

Three observers (one of the authors, WS and two naïve observers, RC and JW) with normal or corrected-to-normal vision participated in the experiment.

2.1.2. Stimuli

The experiment was conducted under dim light with a viewing distance of 57 cm constrained by a chin rest. The stimuli were displayed on an Apple Color monitor (600×400 pixels, 67 Hz refresh) controlled by a Macintosh G4 computer. All stimuli were presented on a black background (0.1 cd/m^2). The fixation point was a white dot with a radius of 4.7′ (42.6 cd/m^2) displayed at the center of the screen.

The cyan-colored disc (7.5 cd/m^2) used to induce apparent motion had a radius of $0.6°$ and was presented at eccentricity of $6.4°$. The two discs, consisting of a motion sequence, were horizontally separated by $7.8°$ center to center. The size of the reference bar and the test flash was $0.1° \times 0.9°$ and the test flash was presented with $3.9°$ of separation from the disc into the periphery (eccentricity of $9.3°$). The additional flash (foil) of the same size as the test flash was located such that it was vertically aligned with the fixation dot and horizontally aligned with the test flash. The vertical distance between the reference bar and the test flash was $10°$ center to center.

2.1.3. Procedure

The basic task procedure was shown in Fig. 1b. After observers initiated a trial, a reference bar, which remained on the screen during the trial, appeared in the periphery of one of the four quadrants. The chosen quadrant depended on the direction of motion (left to right or right to left) and on the visual field (upper or lower) tested. Observers continued to fixate on the dot at the center of the display while apparent motion between two discs was repeated. No eye movements were allowed. Even though we did not monitor the eye movements, all observers were experienced psychophysical observers and were highly confident about their fixations throughout the task.

Apparent motion was achieved by alternating a disc in one of the four quadrants with another disc at the horizontally adjacent quadrant so that horizontal apparent motion across the center was seen for each trial in the upper or lower visual field. Each disc was presented for 30 ms with 240 ms ISI (inter stimulus interval) within a cycle of apparent motion, and three cycles of motion were repeated per trial with 1500 ms interval between cycles. Because of this timing, three cycles of unambiguously unidirectional horizontal motion were observed for each trial. Observers were required to track the discs with their attention. Two different directions of motion were alternated every other trial (left to right or right to left) within a block and the upper and lower fields were tested in a separate block.

On the third cycle of apparent motion, a test flash was presented for 15 ms beyond the location of the second disc in the direction of the motion. The time intervals between the onset of the first disc of the apparent motion and the test flash (SOA) varied; seven SOAs (30 ms, 60 ms, 120 ms, 150 ms, 180 ms, 240 ms, and 270 ms) were chosen to be tested. To reduce the integration of the flashes into the apparent motion sequence, an additional flash was displayed simulta-
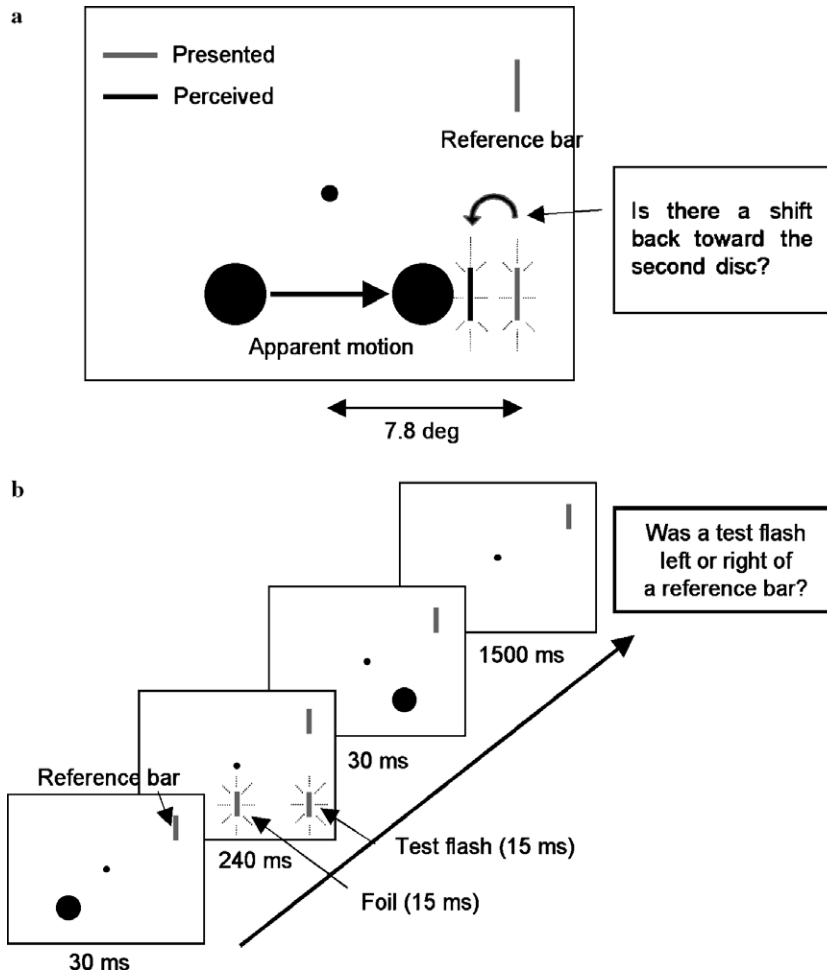
Fig. 1. (a) A schematic view of stimulus configuration and perception of a position shift: when a test flash was presented beyond the end point of apparent motion it was perceived closer to the second disc than its veridical position. (b) A sample trial event for Experiment 1. Apparent motion was induced by two discs alternating with 240 ms ISI. A test flash was presented for 15 ms with an additional flash at the center (foil) varying SOA (time interval between the onset of the fist disc and the test flash).

neously with the test flash in the middle of the apparent motion path. The extra flash and the reference bar were offset together with the test flash. Observers were asked to determine whether the test flash appeared to the left or right of the reference bar (method of constant stimuli, two alternative forced choice task). The horizontal physical offset between the reference bar and the test flash was varied in nine steps. The threshold of perceived alignment at which observers reported the location of the test flash in the direction of the second disc at 50% was calculated by Probit analysis (Finney, 1971) from the psychometric functions. Four estimates (each based on 36 trials) of the psychometric function contributed to the standard errors.

2.2. Results

Because the effects of motion direction (left to right or right to left) and of the visual field (upper or lower) themselves were not of interest in this experiment, we combined the data from the two directions of motion and from the two visual fields for the data analysis.

The data illustrate the main finding: the test flash presented beyond the location of the second disc was substantially mislocalized back toward the second disc. All three observers' data showed a similar pattern. After the onset of the first disc, the illusory shift effect increased with SOA, peaked between 100 ms and 200 ms SOA, and then gradually decreased thereafter (Fig. 2). These results are clear evidence for a position shift beyond the end point of apparent motion. It is important to note that this shift of location is *opposite* to the direction of motion, whereas all results from previous research for position distortion along the motion path lying before the end point of motion have been in the *direction* of the motion. This may be evidence of a compression effect elicited by apparent motion where the perceived locations of static stimuli are pulled toward the end point of the motion.

3. Experiment 2

Experiment 1 showed that, when a test flash was placed beyond the end point of an apparent motion, its location appeared shifted back toward the end point. In order to
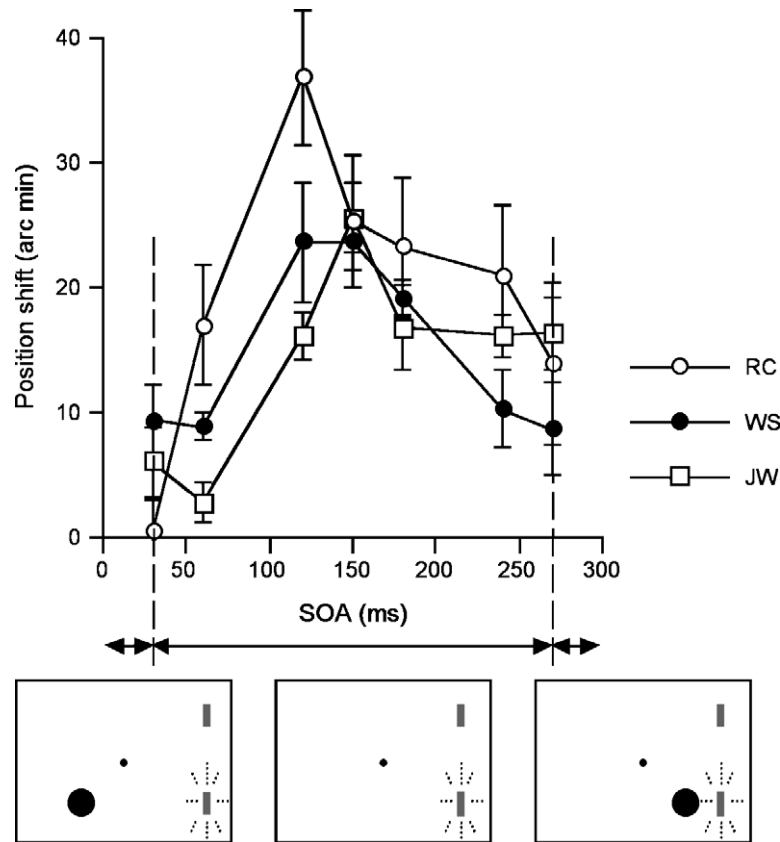
Fig. 2. Position shift as a function of SOA in Experiment 1 (three observers). Positive values of a position shift mean that the flash was perceived closer to the second disc than its veridical position. The insets below the graph show which frame in the apparent motion sequence were on the screen at the moment of the flash. Error bars indicate ±1 SEM.

examine whether this effect is part of a general compression effect occurring near the end point of apparent motion, which is comparable to bi-directional saccadic compression, it is necessary to test in front and beyond the end point of apparent motion together. Thus, in Experiment 2, we presented the flashes at two more locations in front of the end point (beyond the start point into the periphery and on the apparent motion path) as well as beyond the end point. The results of our first experiment were extended to measure the details of position distortion, presenting the flashes at a larger range of timings relative to the onset of the motion and to the offset. In addition, instead of employing a relative localization task, we used an egocentric localization task by requiring observers to determine the perceived position of the flash without a reference.

3.1. Method

3.1.1. Observers
The same observers as in Experiment 1 participated.

3.1.2. Stimuli
A horizontal line was drawn across the whole screen in the upper or lower visual field (5° above or below the fixation point), running through the discs. A test flash was presented in one of the three positions: (1) −7.8°, which

represents 7.8° away from the midpoint of the horizontal line in the opposite direction of motion (eccentricity of 9.3°), (2) 0°, which is the midpoint of the horizontal line (midway of the apparent motion path), and (3) 7.8°, which is 7.8° away from the midpoint of the horizontal line in the direction of motion (eccentricity of 9.3°). No reference bar was used. All other stimulus specifications were identical to those in Experiment 1.

3.1.3. Procedure
A fixation point and a horizontal line crossing the screen in the upper or lower visual field were presented at the beginning of the trial and remained on the screen throughout the trial. Each trial was initiated with a brief 'beep' sound.

To prevent the integration of the test flashes into the apparent motion sequence, an additional flash was displayed simultaneously with the test flash in the middle of the apparent motion path when the test flashes were presented in either periphery. In order to indicate the location of the test flash, a red arrow (7.5 cd/m^2) pointing either to the left or right was presented 1.6° below the fixation for 600 ms. When the test flash was on the apparent motion path it was presented alone without an extra flash so a red arrow cue was not used. Another 900 ms later, apparent motion between two discs was repeated twice in the upper

or lower visual field. The observers were asked to track the motion of the discs with attention and no eye movements were permitted.

On the third cycle of the apparent motion, a test flash was presented in one of three positions (beyond the start point into the periphery, on the motion path, beyond the end point into the periphery). Directions of motion (left to right or right to left), flash positions, and the time interval between the onset of the first disc of the apparent motion and the test flash (SOA: 30 ms, 60 ms, 120 ms, 150 ms, 180 ms, 240 ms, and 270 ms) were all randomly varied within a block. The upper and lower fields were tested in separate blocks.

After the second disc was offset on the third cycle of motion, the mouse cursor appeared at the fixation point. Observers were asked to report the perceived position of the test flash by dragging the mouse and clicking on the perceived position on the horizontal line. The horizontal line did not have any ticks on it and was presented only to

make the observers' responses have roughly the same vertical coordinates. The trial was terminated when the observer clicked the mouse. A total of 16 measurements were made for each SOA in each test location.

3.2. Results

In this experiment, we were able to demonstrate bi-directional compression toward the end point of apparent motion. The flashes in front of and beyond the second disc all appeared displaced toward the end point of apparent motion (Fig. 3). In the former case (i.e., either when the flash was further away from the start point into the periphery or when it was on the motion path), flashes were mislocalized in the direction of motion. In the latter, flashes were displaced back toward the end point.

Taking into account the baseline mislocalization of each observer (indicated by the dashed line in Fig. 3), we
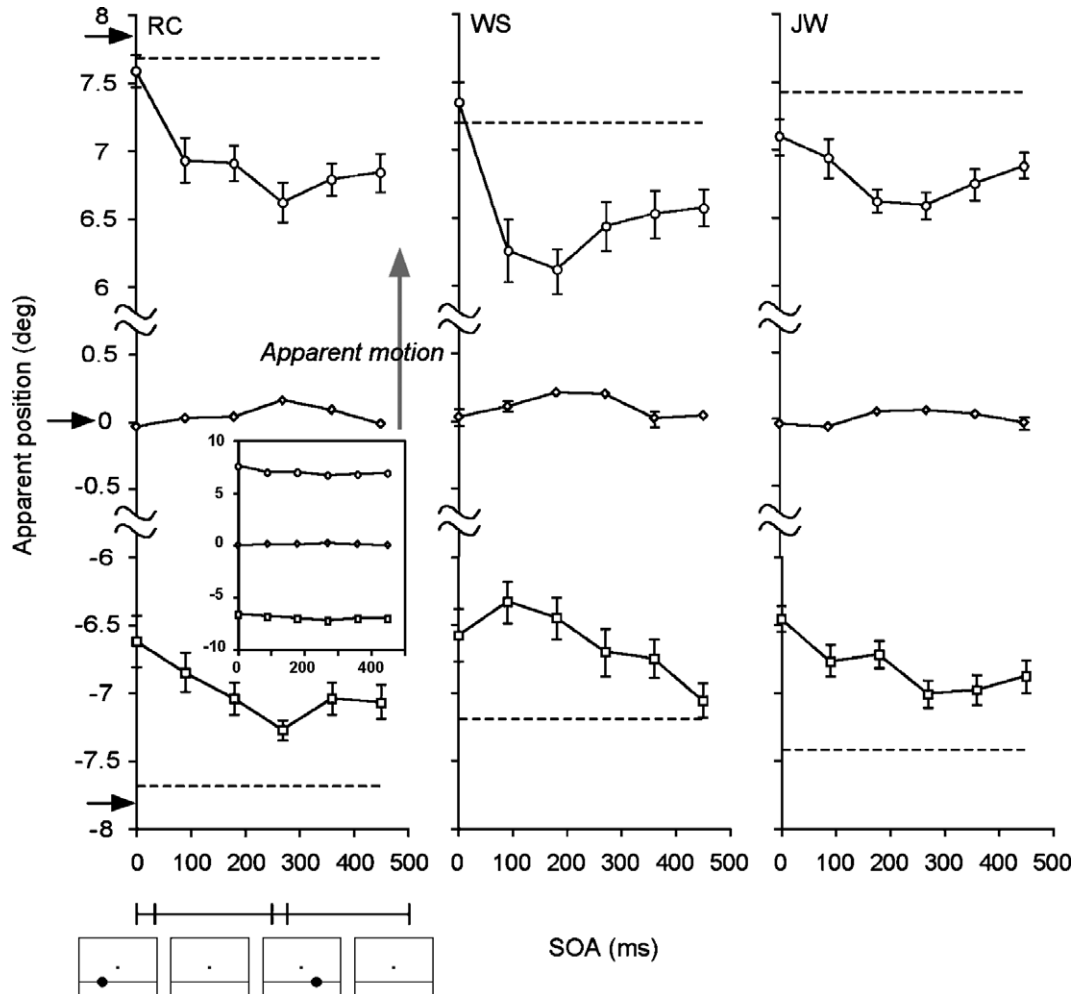

Fig. 3. Perceived positions of flashes at three test locations. The *X*-axes show the time of the flash relative to the onset of the first disc and the *Y*-axes show the apparent position of the flash. Each panel shows the data from one observer, RC, WS, and JW, respectively. Apparent motion was shown between the discs 3.9° to the left or right of the midpoint of the horizontal line presented in the upper or lower visual field. The gray arrow between the left and the middle panel indicates the direction of apparent motion. The flash was presented at −7.8° (open squares), 0° (open diamonds), and 7.8° (open circles). The physical location of the flash is indicated by three arrows to the left of the *Y*-axis. The perceived positions of three flashes are plotted on the uncompressed *Y*-axis in the inset in the left panel. The inset under the left panel indicates which motion display was on the screen at the moment of flash. Error bars show ±1 SEM.

estimated that the size of the maximum compression effect on the flashes in either side of periphery was around 1° and was almost the same for all three observers. This value is about three times as large as in Experiment 1 (but about a factor of 10 smaller than saccadic compression effects, Morrone et al., 1997; Ross et al., 1997). The difference in magnitude between our first and second experiments may have arisen from the difference in the spatial judgment tasks used. Localization could be more accurate when the judgment was made in relation to other references rather than in an egocentric spatial frame without a reference.

For the flash beyond the end point (7.8°), it should be also noted that the time course of the effect was different from Experiment 1. Whereas, in Experiment 1, the mislocalization effect reached the peak near 150 ms SOA and returned almost to the baseline around 250 ms SOA, showing a sharp rise and fall, the effect was rather slowly built up from the onset of the fist disc, peaked around the time of the onset of the second disc (100 ms to 300 ms SOA, depending on the observer), and decreased rather gradually thereafter in Experiment 2. The illusory shift was not completely corrected even at the longest SOA in the present experiment. This discrepancy might arise from different methods measuring the perceived location of a test. In Experiment 1, the location of the test flash was compared to the reference bar (relative judgment), while the perceived location of the test was measured in an egocentric fashion without a reference in Experiment 2. Without an explicit reference, the most salient reference would likely be the fixation point which remained on the screen throughout the trial. Using a similar localization method (pointing to the location of a target) to the one that we used, Sheth & Shimojo (2001) found that the briefly flashed target was perceived shifted toward the center of gaze and salient landmarks and the size of the effect increases as time interval between target presentation and localization judgment increases. If this shift toward the salient landmarks in view which grows larger over the course of time was combined with the more transient compression effect we reported in the previous experiment it could result in rather sluggish time course of the effect observed in Experiment 2.

The flash presented midway on the apparent motion path (0°) was also shifted toward the end point of motion, which is consistent with our previous finding that the flashes presented on the apparent motion path were displaced in the direction of the motion (Shim & Cavanagh, 2004). However, probably because of the salient vertical alignment cue with the fixation, the magnitude of the shift is not as large as with the peripheral flashes. On the other hand, the time course of the effect was similar to that observed for the flash beyond the end point.

For the flash beyond the start point (−7.8°), it was also mislocalized in the direction of apparent motion. The effect was maximal at the onset of the first disc, and after this point began to weaken. In the flashes both beyond the start and end point, we identified the compression effect for almost all SOAs that were tested except for the shortest

SOA for the flash beyond the end point. (One of the observers, WS, also did not experience the effect at the longest SOAs for the flash beyond the start point).

This spatial compression toward the end point of motion resembles bi-directional compression toward the saccade target induced by eye movement, although it is far smaller in magnitude. The relationship between the two types of compression and the role of attention and planned eye movements will be discussed further as possible common underlying mechanisms in both effects.

4. Experiment 3

In the previous experiments, the test flash could have been integrated into the apparent motion to the second disc, despite our attempt to prevent this by presenting the extra flash (foil) on the middle of the motion path between the two discs. It may be that, as in the *Fröhlich* effect (i.e., the shift of initial position in the direction of motion, Fröhlich, 1923), apparent motion from the flash to the second disc would produce a shift of the test flash toward the end point of the motion. To test this alternative, a control experiment was performed where all the experimental stimuli and procedures were identical to those for Experiment 1, except that the first disc was not displayed so that the only remaining apparent motion, if any, was the one from the test flash to the second disc.

4.1. Method

4.1.1. Observers
The same observers in Experiment 1 participated.

4.1.2. Stimuli
The stimuli and experimental procedure were identical to Experiment 1 except that the first disc was not presented.

4.2. Results

When no first disc was presented, we observed significantly reduced position shifts of the test located beyond the second disc (now the only one presented) as compared to the original effect. For comparison, the data from the first experiment is shown in parallel with the data from the current experiment (Fig. 4). The time courses as well as the sizes of the effects are in marked contrast to the effect in two previous experiments. Obliterating apparent motion between the discs considerably reduced the magnitude of position distortion. Based on such clear differences between the data from the present and previous experiments, we conclude that illusory shifts back toward the end point of apparent motion is not due to the *Fröhlich* effect but is a consequence of the apparent motion seen between the first and second disc.

In an additional control experiment, using a relative position judgment task between two flashes without an apparent motion display, we tested the possibility that the
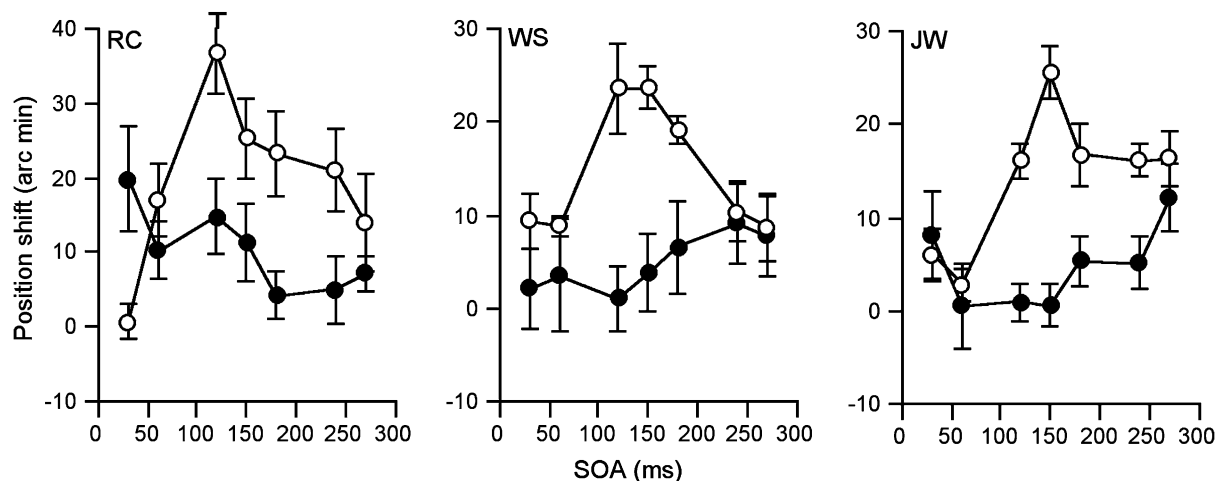
Fig. 4. Position shifts from three observers in Experiment 3: closed circles show the effect in Experiment 3. The results of Experiment 1 are also presented for comparison (open circles). Error bars represent ±1 SEM. To make the SOA at which the flash was presented comparable to the first experiment, SOA was defined as the time interval between the onset of the trial and the test flash in Experiment 3.

basic foveal mislocalization effect (when gaze is maintained at a fixation point, the perceived position of a target in the periphery appears to be more foveal than its veridical position) contributed to the result (Mateeff & Gourevich, 1983; Mitrani & Dimitrov, 1982; Müsseler, van der Heijden, Mahmud, Deubel, & Ertsey, 1999; van der Heijden, van der Geest, de Leeuw, Krikke, & Müsseler, 1999). Without apparent motion, we found no significant localization bias, which ensured that the effect was not caused by a baseline bias toward the fovea during eye fixation.

5. Discussion

The present study has demonstrated that illusory position shifts around the end point of apparent motion are not uniform. While an object flashed in front of apparent motion appears shifted in the *direction* of motion, the same object is mislocalized in the *opposite* direction to the motion when it is presented beyond the apparent motion end point. Our control experiments ruled out the possibility that this position shift effect was caused by misperception of the initial point in apparent motion from the test flash to the second disc as in the *Fröhlich* effect or baseline mislocalization toward the fovea.

Such bi-directional spatial compression toward the end point of motion mirrors saccadic compression where the perceived position of spatial elements appears shifted toward the eye movement target (Lappe et al., 2000; Morrone et al., 1997; Ross et al., 1997). We propose attention and planned eye movement signals as two possible common mechanisms underlying both the apparent motion-induced compression reported here and the saccadic compression.

The role of attention in illusory position shifts has been previously suggested in studies on the influence of high-level motion on position distortion (Shim & Cavanagh, 2004, 2005; Watanabe, Nijhawan, & Shimojo, 2002; Watanabe, Sato, & Shimojo, 2003). For instance, Shim &

Cavanagh (2004) show that illusory position displacements could be induced by perceived apparent motion. In their experiment, the stimulus consisted of four discs: two discs were located at the diagonally opposite corners of an imaginary square, alternating with the discs at the other two corners. The resulting percept is bistable so that, at any given moment, the perceived motion can be either horizontal or vertical without any change in the physical properties of the stimulus. Position shifts were found only when the test flashes were placed on the perceived motion path. Position distortions in this study were attributed to high-level apparent motion, which was perceived along one path at a time. Taking the view that apparent motion is caused by the displacement of attention from the first location to the second (Horowitz & Treisman, 1994; Shioiri, Yamamoto, Kageyama, & Yaguchi, 2002; Verstraten, Cavanagh, & Labianca, 2000; Wertheimer, 1912), the authors have suggested that the distorted percept of visual space was produced by a shift of attention between the two elements of apparent motion.

The idea of attention-based compression is also useful in explaining other types of position distortions. A number of studies have shown that the perceived position of an object is pulled either toward the center of gaze (Mateeff & Gourevich, 1983; Mitrani & Dimitrov, 1982; Müsseler et al., 1999; van der Heijden et al., 1999) or toward salient visual landmarks in the visual field (Deubel, 2004; Lappe et al., 2000; Sheth & Shimojo, 2001). Because the focus of attention usually coincides with the fixation point or with salient visual features in view, it is possible that attention might have played a role in creating a spatial bias in these experiments. In fact, there is neurophysiological evidence that a salient object in the visual field automatically activates attentionally modulated cells in posterior parietal areas even when we do not voluntarily allocate attention to that object (Constantinidis & Steinmetz, 2005; Gottlieb, Kusunoki, & Goldberg, 1998). Since most of the landmarks in the previous saccadic compression studies are often the

only salient reference points in otherwise uniform backgrounds, it may be that these features draw spatial attention, leading to bias toward the focus of attention.

However, it is important to note that the effects observed in these experiments were much smaller than those of saccade-induced compression (50% gain in saccadic compression vs. 6∼12% gain in apparent motion-induced compression). One possibility is that eye movements provide a clear reference signal to time lock the analysis of position effects to the actual eye movement behavior. In contrast, the analysis for the apparent motion are time-locked to the physical stimulus and not the attentional shifts they produce. The actual shifts in attention may have much more variable time course, reducing the strength of the averaged position shifts, since they are not so well aligned in the stimulus locked data. Another important possibility is that, although no eye movements were allowed in the experiments, the observed effect might have arisen from covertly planned eye movements to the end point of apparent motion. Whereas spatial compression in saccades could result from either eye movement planning or the execution of the saccade (or both), apparent motion-based compression could be induced by signals from planned eye movements to the end point of motion. While the effects of planning alone without execution might be smaller, as the present findings show, they are in accordance with those for executed eye movements.

Given the close relationship between eye movements and attention demonstrated with extensive evidence from psychophysics, neurophysiology, and functional neuroimaging (for psychophysics: Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995; for neurophysiology: Moore, Armstrong, & Fallah, 2003; Moore & Fallah, 2001, 2004; for neuroimaging: Corbetta et al., 1998), the influence from attention and eye movement would not be easily separable. It has also been intensely debated whether, as the premotor theory of attention has suggested (Sheliga, Riggio, & Rizzolatti, 1994), the purpose of attention is solely target selection for motor activities, or whether attention exists as an independent system from the motor system (Murthy, Thompson, & Schall, 2001; Sato & Schall, 2003; Thompson, Bichot, & Schall, 1997). Though this is a central issue, it lies beyond the scope of our study.

What are the underlying neural substrates for the compression effect? It has been reported that, in the lateral intraparietal area (LIP), shifts of the receptive field to the eye movement target occur prior to the saccades (Duhamel, Colby, & Goldberg, 1992). This local receptive field remapping according to the coordinates provided by an impending saccade provided a possible neurophysiological basis for saccadic compression (Morrone et al., 1997; Ross et al., 1997; VanRullen, 2004). As an alternative to the transformation of spatial coordinates, Hamker (2003) has recently proposed that attention signals indicating the planned eye movement in the frontal eye fields (FEF) can provide feedback information into visual cortices to modulate the retinal coordinates (Hamker, 2003). The present findings support such attention and planned eye movement-based models of saccadic compression.

In conclusion, we showed that position distortion caused by motion is not uniform, specifically the perceived position of a flash appears to be closer to the terminal point of apparent motion irrespective of whether it is presented in front or beyond the end point of the motion. The correspondence between compression toward the end point of apparent motion and saccadic compression toward the saccade target suggests that attentional shifts or planned eye movement signals may play a role in both.

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