

The motion-induced position shift depends on the perceived direction of bistable quartet motion

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Abstract

Motion can influence the perceived position of nearby stationary objects (Nature Neuroscience 3 (2000) 954). To investigate the influence of high-level motion processes on the position shift while controlling for low-level motion signals, we measured the position shift as a function of the motion seen in a bistable quartet. In this stimulus, motion can be seen along either one or the other of two possible paths. An illusory position shift was observed only when the flashes were adjacent to the path where motion was perceived. If the flash was adjacent to the other path, where no motion was perceived, there was no illusory displacement. Thus for the same physical stimulus, a change in the perceived motion path determined the location where illusory position shifts would be seen. This result indicates that high-level motion processes alone are sufficient to produce the position shift of stationary objects. The effect of the timing of the test flash between the onset and offset of the motion was also examined. The position shifts were greatest at the onset of motion, then decreasing gradually, disappearing at the offset of motion. We propose an attentional repulsion explanation for the shift effect.

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Encoding positional information of objects is vital for visual perception in our daily interaction with the environment. In taking actions necessary for survival, such as capturing prey, avoiding predators, or approaching potential mates, it is essential to accurately localize the positions of an object.

The theories of local sign and labeled lines were proposed in the 19th century (Hering, 1899; Lotze, 1886; Müller, 1826; von Helmholtz, 1962) to account for the encoding of position in the visual field. The idea is that each receptor on the retina is attached to a specific nerve fiber, which is connected to a retinotopically organized map in the brain; thus, the distinct neural pathway beginning with a given location on the retina continues to indicate that specific location for higher level processing. This idea of labeled lines and signs has been supported, with some modification, by single-cell recordings and fMRI studies demonstrating multiple retinotopic maps in the brain.

However, there have been several studies showing that this simple view is incorrect, and that other factors besides the retinal location of an object play an important role in encoding its positional information. One clear example illustrating this point is the position distortion caused by eye movements (Cai, Pouget, Schlag-Rey, & Schlag, 1997; Matin, 1972; see Ross, Morrone, Goldberg, & Burr, 2001; Schlag & Schlag-Rey, 2002 for review). Ross, Morrone, and Burr (1997), for example, showed striking shifts and compressions of location in stimuli presented just prior to a saccade. An object's motion also appears to affect its perceived position, further suggesting the perceived position is not completely retinotopically mapped but is determined by integrating other sources of information (DeValois & DeValois, 1991; Fröhlich, 1923; Nijhawan, 1994; Ramachandran & Anstis, 1990; Schlag, Cai, Dorfman, Mohempour, & Schlag-Rey, 2000; see Kregelberg & Lappe, 2001; Nijhawan, 2002; Whitney, 2002 for review).

Recent work, moreover, has shown that motion can alter not only the perceived position of the moving stimulus itself but also that of nearby static stimuli

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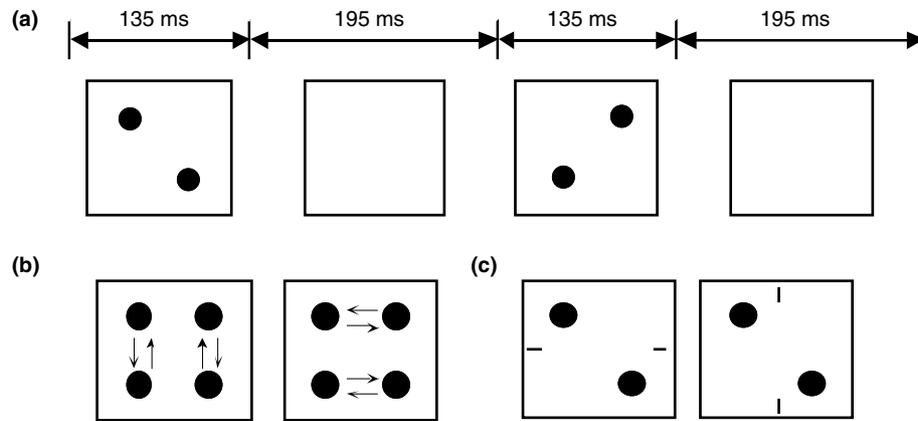


Fig. 1. (a) Bistable quartet sequences in experiment 1: two discs at two diagonally opposite corners of an imaginary square were alternated with two discs at the other corners with 195 ms ISI, (b) either horizontal or vertical motion was seen. (c) The test flashes were presented either on the left and the right sides of the square defined by the four discs or on the top and the bottom sides.

(Whitney & Cavanagh, 2000). In these experiments, briefly presented stationary flashes appear to be shifted in the direction of motion of the distant stimulus. This result implies that the apparent position of a stimulus is influenced by motion signals regardless of whether these signals originate from the stimulus itself or from other nearby stimuli.

This research raises a further important question about the nature of the motion processes affecting the position encoding of objects. In the motion perception literature, two largely different motion systems have been proposed (Anstis, 1980; Braddick, 1980; Cavanagh & Mather, 1989; Julesz, 1971; Lu & Sperling, 1995). One is a low-level motion system assumed to extract energy- or velocity-based motion signals from the passive responses of local motion detectors. The other is a high-level motion system, which requires object-token matching and tracking a target's changing position with attention. Since, in Whitney and Cavanagh's (2000) original report of flash shift effect, motion perception was induced by rotation or translation of sinusoidal luminance gratings, in which the low-level motion energy of the stimulus is always consistent with any high-level percept of motion, it is difficult to separate the contributions from each motion system. Therefore, the question of whether the high-level percept of motion alone can cause this position shift, when the low-level spatio-temporal properties of the motion stimulus are controlled for, remains to be investigated. Two recent papers have addressed the role of high-level motion in the position shift using motion viewed through apertures (Watanabe, Nijhawan, & Shimojo, 2002) and inferred motion (Watanabe, Sato, & Shimojo, 2003), and we now add to these studies with a paradigm that clearly isolates high-level motion processes.

To examine the independent contribution of high-level motion, we chose the 'bistable quartet' (Ternus, 1938). Two spots of light are presented simultaneously

at two diagonally opposite corners of an imaginary square for a brief moment; after some time interval, the two other spots are flashed at the other two opposite corners (Fig. 1(b)). For displays with discs that are closely spaced, the alternating discs will stimulate the receptive fields of directionally selective units in early visual areas, such as V1, V2, V3, V3A, or MT. In this case, low-level motion signals are balanced or ambiguous, as units responding to both horizontal and vertical will be equally activated. However, if the distance between the discs is too large to stimulate individual motion detectors, there will be little or no low-level response. In this case, the motion impressions, which remain robust, must depend on high-level motion processes. These processes interpret the motion in the quartet stimulus as falling on either of the two possible paths, horizontal or vertical, but along only one path at a time. With the relative distance between the discs properly balanced, observers find that the path of the perceived motion can alternate spontaneously between the two directions, being horizontal for several alternations, then vertical. With some practice, observers can make the direction seen in these balanced displays switch at will. As many have shown, the perceived direction can be biased by changing the horizontal or vertical distances between the discs (Ramachandran & Anstis, 1983, 1986; Ternus, 1938).¹ In our experiments, the horizontal and vertical spacing were always equal

¹ To check that this bistable quartet stimulus produces little or no low-level motion response, we tested a static motion aftereffect (MAE) on the apparent motion path using the asymmetric timing of experiment 2 that produces a motion impression in only one direction. The test was a thin band of 40% contrast sine wave grating lying along the apparent motion path extending from the first disc to the second and having height equal to the disc diameters and a spatial frequency of 1 cpd. After 30 s of adaptation, none of the three observers we tested (AH, WS, and JW) saw any MAE on this test.

and were large enough (7.83° at eccentricity of 5.54°) to ensure that few if any low-level detectors could respond.

To test the effect of high-level motion on position, we briefly presented two flashes adjacent to the vertical or horizontal edges of the quartet and measured the shift in perceived location of the flashes. Critically, we evaluated the perceived shift as a function of whether the flashes were adjacent to the side of the quartet where motion was being seen on that trial. If the direction of illusory position shift depends on the location of apparent motion in the quartet, it would suggest that the high-level motion process does indeed influence position encoding of stationary objects. Also, we examined not only the general influence of high-level motion on the position shift effect but also the timing of the effect. In experiment 2, we measured the strength of the position shift over the time course of the motion.

Based on our results, we suggest that attentional repulsion (Suzuki & Cavanagh, 1997) underlies the position shift effect.

1. Experiment 1

1.1. Method

1.1.1. Observers

Two observers (one of the authors and one naïve observer) with corrected-to-normal vision participated in the experiment.

1.1.2. Stimuli

The observers were tested in a dimly lit room with a chin rest 57 cm away from a high-resolution Apple Color monitor (600×400 pixels, 67 Hz refresh) controlled by a Macintosh G4 computer. All stimuli were presented on a black background (0.10 cd/m^2). The fixation point was a white dot with a radius of $4.7'$ (50.6 cd/m^2) displayed at the center of the screen. The radius of each cyan-colored disc (9.53 cd/m^2) was 0.5° and the distance between the center of two horizontally or vertically adjacent discs was 7.83° . The length and the width of the test flashes were 0.9° and $4.7'$ respectively. The test flashes were presented at the midpoint of two opposite sides (either left and right or top and bottom sides) of a square defined by the four corners of the quartet (Fig. 1(c)). The distance between the inner edge of the flash and the nearby side of the imaginary square was $7.05'$ so that the flashes were placed just outside the apparent motion path.

1.1.3. Procedure

After initiating a trial, one pair of discs were presented simultaneously at two diagonally opposite corners of an imaginary square for 135 ms; after 195 ms ISI (inter stimulus interval), the other pair of discs were flashed at

the other two corners for 135 ms (Fig. 1(a)). The motion cycle was repeated by presenting the first pair again after 195 ms ISI until the response was made. The percept was bistable so that either a horizontal or a vertical direction of apparent motion was possible at any given moment. However, observers were asked to will themselves to see only one of the two possible directions of motion (either vertical or horizontal) for a given trial. If observers found that the motion was perceived in the direction other than the one they had been asked to see during a given trial, observers were asked to wait until the perceived direction changed back to the instructed direction before they continued judging and nulling the misalignment of the flashes. The correspondence between the observer's perceived direction of motion and the instructed direction of motion was confirmed at the end of each trial by asking the observer to report the perceived direction of motion during the adjustment. In all trials, all observers saw the instructed direction for duration sufficient to make an acceptable setting. Within a trial, the two, initially physically aligned flashes were presented for 30 ms at a fixed SOA within each cycle (Fig. 1(a) shows the four frames of one cycle) over the course of many cycles in a method of adjustment procedure. The motion in the quartet alternated back-and-forth along the perceived direction during each cycle; however at a fixed SOA, the motion during the flash was always the same direction, for example, always rightward for horizontal, or always downward for vertical. The time between the presentation of the first pair of quartet and the test flashes (SOA) were systematically varied; eight SOAs (45, 105, 210, 270, 375, 435, 540, and 600 ms) were tested such that two SOAs were selected from within each of four frames of the cycle (the first pair of discs, ISI after the first pair, the second pair, and ISI after the second pair). While fixating on a center dot, observers adjusted the position of the right flash relative to the left flash or the bottom flash relative to the top flash by pressing the assigned keys until they appeared aligned over repeating cycles of quartet motion. The instructed direction of quartet motion (vertical or horizontal) and the location of the flashes (left and right sides or top and bottom sides) were fixed within a block.

The measurement of the illusory shift was taken as the physical misalignment of the flashes when the observers self-terminated the trial. For each block, 8 trials were run in a randomized order (a trial for each SOA). Observer completed 32 blocks in total providing 8 measurements for each combination of conditions (SOA (8) \times quartet motion (2) \times location of the flash (2)).

2. Results

When the perceived motion of the quartet was vertical, the two motion paths joined the two discs on the left

side and the two discs on the right side whereas the path joining the two top discs and the two bottom discs had no motion. As shown in Fig. 2, the two flashes presented at the midpoint of the left and right side showed a considerable vertical misalignment in the direction of the motion when perceived motion was vertical. However, when the perceived direction of motion was hori-

zontal, following paths along the top and bottom sides of the quartet, there was no illusory displacement for these same flashes. In contrast, the test flashes presented to the top and bottom sides of the imaginary square were displaced when the perceived motion was horizontal but not when it was vertical (Fig. 3). Even though there was no change in the physical stimulus, the posi-

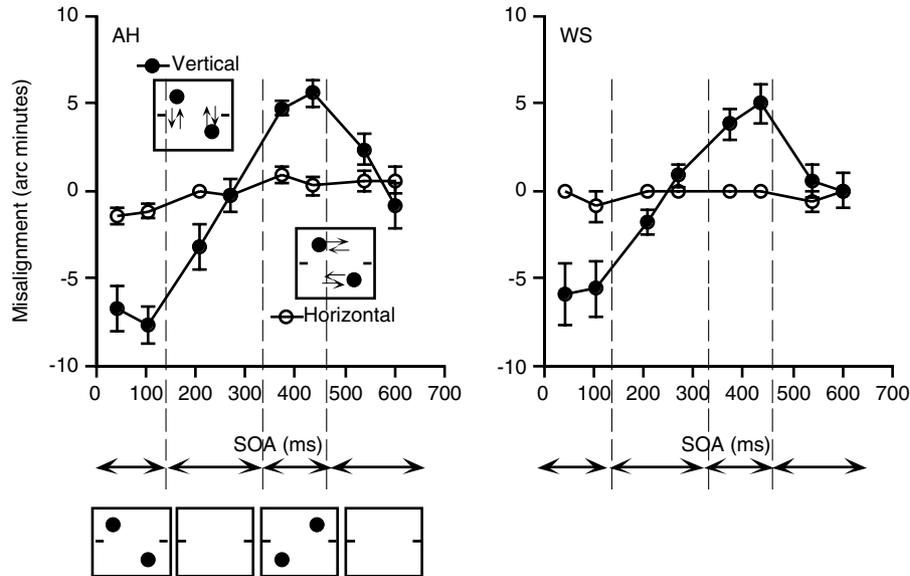


Fig. 2. Experiment 1: Position shift of the flashes presented on the left and the right sides of the quartet as a function of SOA for two observers. The ordinate shows the perceived misalignment of the two flashes in arc minutes. Since the misalignment was measured by subtracting the position of the left flash from that of the right flash, a negative value indicates that the left flash appears to be lower than the right flash and vice versa for a positive value. The abscissa shows the time (SOA) between the presentation of the first pair of the disc and the test flashes. Filled circles indicate the misalignment when the quartet appeared to be moving vertically and open circles indicate the misalignment when the quartet appeared to be moving horizontally. Insets depict the percept of the quartet's motion. The figures below the graph show which frames in the sequence were on the screen when the flashes were presented. Error bars represent ± 1 S.E.M.

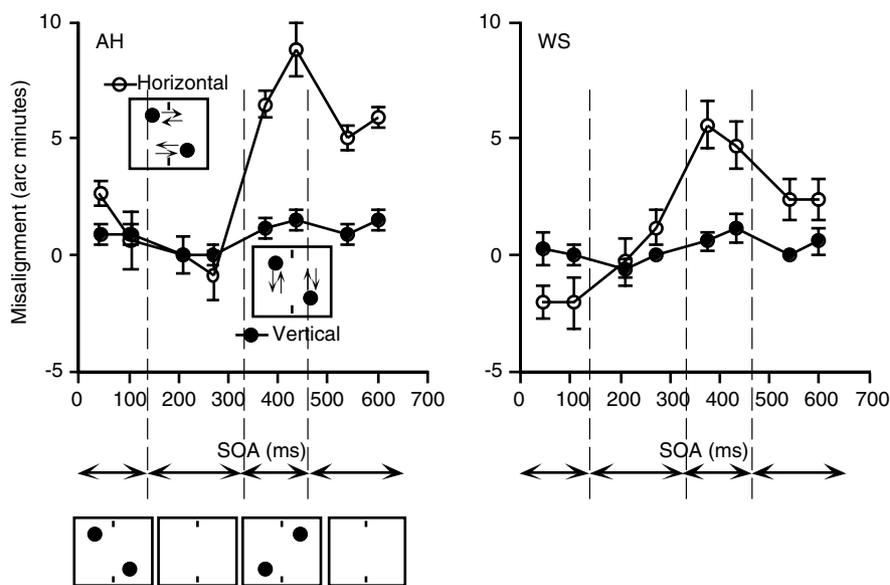


Fig. 3. Experiment 1: Position shift of the flashes presented on the top and the bottom sides as a function of SOA for two observers. Since the misalignment was measured by subtracting the position of the upper flash from that of the lower flash, a negative value indicates that the lower flash appears to be more on left than the upper flash and vice versa for a positive value. Error bars represent ± 1 S.E.M.

tion shift of the test flashes was determined by the perceived direction of motion—as the motion organization changed, so did the location where the illusory position shifts were seen.

Although it is still not clear the extent to which low- and high-level motion process contribute to the position shift when both motion signals coexist in the same stimuli, this result showed that high-level motion on its own is sufficient to produce the position shift.

One noteworthy point in these data is that the largest illusory position shift occurred when the flashes were presented with the discs or immediately after they disappeared, that is, at the moment the motion reversed from up to down or left to right. The fact that illusory shift was maximal at the reversal point of the motion led us to examine whether the illusory shift was caused by the motion leading up to the reversal point or the motion starting from that point. This question and the modulation of the effect depending on the time course of apparent motion were examined in experiment 2.

3. Experiment 2

3.1. Method

3.1.1. Observers

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

3.1.2. Stimuli

The stimuli were the same as those used in experiment 1, except for the longer second ISI and simultaneous presentation of all four flashes.

3.1.3. Procedure

Two pairs of discs were presented alternately with two different ISIs; the first ISI was 195 ms, the same as in experiment 1, and the second ISI was a longer pause of 1500 ms. As a result of this asymmetrical ISI, only one direction of motion was seen on each side (left and right sides in vertical motion and top and bottom sides in horizontal motion) depending on which pair of discs was displayed first. In the first sequence, for example, the stimulus in Fig. 1(a) would appear to move left to right on the top if the subject were seeing horizontal motion. In the second sequence, however, the two frames were reversed so the subject would see right to left motion on the top. This reversal of the motion direction depending on the display sequences was also the same for vertical motion. To avoid motion after-effects, two different display sequences (upper left and lower right disc first or upper right and lower left disc first) were alternated every trial.

Again, as in experiment 1, the observers reported whether they had perceived the motion along the instructed path or not. If observers found that the motion was not the one they had been asked to see for that trial, the trial was excluded from the data analysis and an additional trial was run. Average rate of replaced trials was 2.2%, 5.4%, and 4.8% for observers WS, JW, and SK, respectively.

After initiating a trial, to establish the stable perceived direction of motion as instructed, two cycles of motion were repeated before the test flashes were presented. Then, on the third cycle, the flashes were presented at all four locations (the midpoint of top, bottom, left, and right side). This simultaneous presentation of both pairs of flashes was made in order to control for possible influence from the flashes on apparent motion. Observers judged misalignment of appropriate pair of flashes (flashes on left and right sides or flashes on top and bottom sides) for a given trial. The instructed direction of quartet motion (vertical or horizontal) and the location of the flashes (left and right sides or top and bottom sides) remained the same within a block.

The method of constant stimuli with 2AFC (alternative forced choice task) was used: observers judged whether the right flash appeared above or below the left flash, or the bottom flash appeared left or right to the top flash depending on a given block of trial. The physical offset of the pair of test flashes was varied in 9 steps and the threshold of perceived alignment at which the observers reported the flash shift in the direction of perceived motion at 50% was calculated with a linear interpolation procedure of the psychometric functions.

Six SOAs (45, 105, 210, 270, 375, and 435 ms) were tested so that two SOAs were selected from the first three frames (the first pair of discs, ISI after the first pair, and the second pair, the second, long ISI was not tested).

Each session consisted of four blocks (direction of quartet motion (2) × location of the flash (2)) and there were 108 trials per block (SOA (6) × flash offset step (9) × display sequence (2)). Observers performed a total of four sessions providing 16 measurements for each threshold.

4. Results

Since neither the effect of different sequences of motion display (upper left and lower right disc first or lower left and upper right disc first) nor the direction of quartet motion (horizontal or vertical) was the main interest, the data for the two display sequences and for two different direction of motion were collapsed (the same pattern was present for both directions of motion). When the flashes were presented on the perceived motion path, the position shift peaked around at the time of

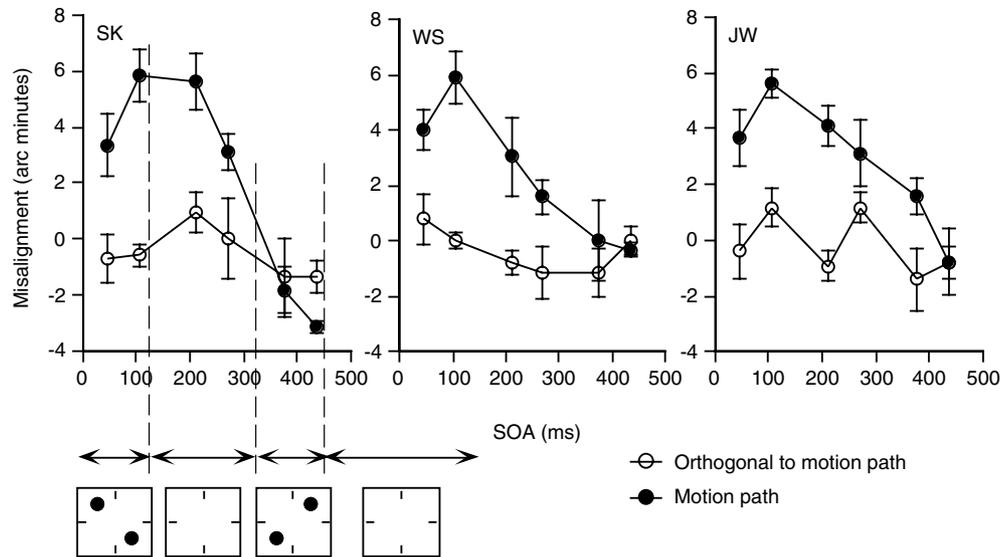


Fig. 4. Experiment 2: Position shift of the flashes as a function of SOA when the test flashes were on the perceived motion path (filled circles) and orthogonal to the motion path (open circles). The ordinate shows the perceived misalignment of the two flashes measured by the displacement of the flashes to null the perceived misalignment. A positive value in misalignment indicates the shift in the direction of perceived motion and a negative value indicates the shift in the opposite direction (in the case of the flashes orthogonal to the perceived motion path, positive and negative values were assigned assuming as if the flashes had been on the motion path). The abscissa shows the time (SOA) between the presentation of the first pair of the disc and the test flashes. The figures below the graph show which motion displays were on the screen when the flashes were presented. Note that observers reported the misalignment of only one pair of the flashes for a given trial even though the flashes were presented at all four locations to prevent possible influence from the flashes on motion perception. Error bars represent ± 1 S.E.M.

the disappearance of the first pair of discs and gradually decreased from this point, as shown in Fig. 4. By the time the end point of motion was reached, the position shift was no longer apparent or had even slightly reversed. If the flashes were presented adjacent to the path orthogonal to the perceived motion, however, no position displacement was shown, which was consistent with experiment 1. These results indicated that the illusory shift of the flashes was caused by the perceived motion that began concurrently with the presentation of the flashes.

Note also that the position shift, even the maximum reported value, was observed for flashes presented before the second pair of discs appeared. This implies the perception of the flashes occurs with a significant delay, at least long enough for the second pair of discs to have appeared and to have generated a motion signal at some level.

5. Discussion

Here we report the use of a bistable quartet to test the role of high-level motion in position coding. The first experiment showed that the perceived position of a flash depended on the perceived motion direction of a bistable quartet: when the motion of the quartet was vertical, flashes on the left and right sides adjacent to the motion path were perceived as displaced in the direction of the motion. Similar displacement was found for flashes at

the top and bottom when the motion was perceived horizontally. However, no position shifts were seen for flashes placed adjacent to the path where no motion was seen. The physical stimulus that led to the vertical or horizontal percept was identical; so the change in the location where the position shift occurred was completely determined by the percept, not by any spatio-temporal properties of the stimulus. This result provides evidence that high-level motion processes are sufficient on their own to produce the position shift of stationary objects.

Testing with a modified quartet further showed the modulation of the effect over the time course of apparent motion; the greatest displacement in the direction of motion occurred when the flashes were presented around the beginning of the motion.

Whitney and Cavanagh (2000) have already shown that the position shift can occur for flashes presented adjacent to very rapidly moving stimuli. These move too rapidly (>8 Hz) for high-level motion to track individual features (Verstraten, Cavanagh, & Labianca, 2000) but nevertheless, position shifts could still be measured adjacent to these motion stimuli. These data indicate that low-level motion alone can produce a position shift whereas our data show that high-level motion alone can also produce a position shift. Watanabe et al. (2002) have addressed the issue of the involvement of high-level motion by using the motion of a diamond seen through a narrow slit. As the diamond crossed over the fixation point in its motion path, a line was flashed in the center

of the diamond. Observers reported that the apparent location of the line was shifted in the direction of the diamond's motion even when the diamond was seen through an aperture as narrow as a single pixel. Clearly, there would be little or no low-level motion in the direction of the diamond when presented through these narrow slits. However, this is a recovery of structure from low-level motion, hence the observation, although consistent with ours, is not completely free of the contribution of low-level motion. Using our bistable motion stimulus with stimulus discs so widely spaced that low-level mechanisms cannot register their displacement, we find that the shift depends on the perceived motion, independently of the spatiotemporal properties of the stimulus, which do not change as the percept changes. We feel that this stimulus best isolates the contribution of high-level motion and the outcome is clear: high-level motion does produce a position shift on its own.

We suggest that attention plays a role in the position shift caused by high-level motion. It is not a new idea that attention is involved in the perception of apparent motion. It was first proposed by Wertheimer (1912) and supported by other recent studies (Dick, Ullman, & Sagi, 1987; Horowitz & Treisman, 1994; Shioiri, Yamamoto, Kageyama, & Yaguchi, 2002; Verstraten et al., 2000). Attention might mediate the motion between the two briefly flashed elements by being drawn first to the initial flash, and then dragged over to the second one.

More importantly, it has been reported that attention at one location can repel the perceived location of briefly flashed tests even over fairly large distances (Suzuki & Cavanagh, 1997). These experiments tested only attention to static elements, not moving ones. It would seem reasonable that if attention were to move, the repulsion field around the focus of attention would move with it, pushing things away in front of it. However, the attentional repulsion effect as originally tested would have to be omnidirectional. There was no reason for it to be stronger in one direction than another and since no moving attention cues were tested, there is no data concerning the nature of the repulsion effect for a moving focus of attention. If omnidirectional repulsion were all there were to it, all test locations ought to show a shift no matter which direction of motion was seen. For example, when the first discs of the quartet appear in the upper left and lower right, attention may be focused on both, and that should cause any briefly flashed test to appear shifted regardless of which direction of motion was seen. To the contrary, the shift was dependent on the perceived direction of motion. The attentional repulsion we propose is, therefore directional, stronger ahead of the motion than to the sides.

For a more direct comparison of our results on motion-based case to original attention repulsion effect, we measured the strength of the original attention repulsion using method of adjustment with the same stimulus used

in experiment 2. In the no-motion case, we presented the flash with only the first frame of the apparent motion display so that no motion was seen along either path. In this display, repulsion of the perceived location of the flash (attentional repulsion) was observed in both directions, vertically and horizontally, an omnidirectional effect of about 5–8 min of displacement, similar in size to the effect reported by Suzuki and Cavanagh (1997). For the motion case, we re-introduced the second motion frame so that apparent motion was seen. Replicating the effect of the main experiment, the flash shift was apparent only for the flash adjacent to the motion path and not for the flash adjacent to the orthogonal path. With the motion present, the shift we measured for the flash adjacent to the path was greater or comparable to (but in the same direction as) the repulsion for the no-motion condition, and the shift for the flash adjacent to the orthogonal path was smaller relative to the solitary condition, decreasing to almost no effect.

This switch from omnidirectional to directional repulsion is a description of the results. We cannot say with certainty whether the position shifts in the two cases are mediated by the same process, one that changes from omnidirectional to directional in the presence of motion. Alternatively, there may be two different processes, an omnidirectional repulsion, seen in both conditions, and a suppression orthogonal to the motion, seen only in the motion condition. Our experiments were not designed to examine which of these explanations is more appropriate. We are piloting further experiments to explore the shape of repulsion field and examine whether apparent motion that includes the test flashes would increase the shift effect (our subjects reported the flashes were not seen as part of the apparent motion).

Watanabe et al. (2003) have examined the idea of attentional repulsion and argue against it; however, we believe that the idea has merit and that their evidence is open to other interpretations. In their main experiment, two rings moved in opposite directions on either side of fixation and two horizontal bars were flashed one on each motion path during their motion. Consistent with the findings of Whitney and Cavanagh (2000), the observers reported a substantial misalignment of the flashes. However, the illusory position shift occurred only when the bar was presented ahead of or on the moving ring. Then, they masked the mid portion of the motion trajectory with an occluding rectangle and found that the illusory displacement of the flashes followed a similar pattern, even while the rings were out of sight (a period of about 350 ms). The authors concluded that inferred motion (Assad & Maunsell, 1995) was sufficient to generate the displacement illusion. To test whether attentional repulsion could account for their result, they presented the rings without any motion, first on one side of the rectangle and then on the other side, duplicating

the timing and positions of the rings (minus the motion) at the beginning and end of their trajectories in the main experiment. Again, here they found the illusory displacement but it was always away from the initial ring location and, unlike the finding in the main experiment, the illusory shift did not change over time during the interval. According to the authors, the unchanging illusory shift in this control condition was the signature of attentional repulsion and they concluded that the very different results during the inferred motion trials could not be due to attentional repulsion.

We agree that Watanabe et al.'s (2003) results show that the illusory shift during their inferred motion trials was not due to attentional repulsion from the attention to the last visible location of the rings. However, it seems more plausible that during the inferred motion trial, attention was not held at the last visible location but traveled along the inferred path and so would, in those trials, produce a time-dependent effect. Watanabe et al.'s result that the illusory shift is reduced once the inferred location of attention passed the test location of the flashes is in close agreement with our results. In our display, the location of the apparently moving target is not behind an occluder but in full view. In both cases, attentional repulsion that moves along ahead of the apparent location of the target will produce the illusory shifts and their change with time that is seen in both studies.

At what locus in the visual system does high-level motion affect position? Recently it has been reported in neurophysiological studies that cell response to the perceived direction of motion in apparent motion stimuli was robust in the lateral intraparietal area (LIP) but less evident in the middle temporal area (MT) (Williams, Elfar, Eskandar, Toth, & Assad, 2003). Based on these findings, we can infer that the high-level motion signals affecting position encoding could originate in the parietal areas.

In summary, this research extends the original finding of the effect of motion on the position-coding process and provides an important clue to the proposed question of the nature of motion processes affecting the position shift effect. Unlike low-level motion system which directly derive motion signal from the local motion detectors, high-level motion has been thought to be involved in identifying object tokens and tracking their position with attention (Anstis, 1980; Cavanagh, 1992; Cavanagh & Mather, 1989; Lu & Sperling, 1995). Because it is the high-level motion processes that produced the position shift effect reported here, we suggest that attention is a contributor to the position shift effect.

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References

- Anstis, S. M. (1980). The perception of apparent motion. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 290, 153–168.
- Assad, J. A., & Maunsell, J. H. (1995). Neuronal correlates of inferred motion in primate posterior parietal cortex. *Nature*, 373, 518–521.
- Braddick, O. (1980). Low-level and high-level processes in apparent motion. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 290, 137–151.
- Cai, R. H., Pouget, A., Schlag-Rey, M., & Schlag, J. (1997). Perceived geometrical relationships affected by eye-movement signals. *Nature*, 386, 601–604.
- Cavanagh, P. (1992). Attention-based motion perception. *Science*, 257, 1563–1565.
- Cavanagh, P., & Mather, G. (1989). Motion: the long and short of it. *Spatial Vision*, 4, 103–239.
- DeValois, R. L., & DeValois, K. K. (1991). Vernier acuity with stationary moving gabors. *Vision Research*, 31, 1619–1626.
- Dick, M., Ullman, S., & Sagi, D. (1987). Parallel and serial processes in motion detection. *Science*, 24, 400–402.
- Fröhlich, F. W. (1923). Über die Messung der Empfindungszeit. *Zeitschrift für Sinnesphysiologie*, 54, 58–78.
- Hering, E. (1899). Über die Grenzen der Sehschärfe. *Berichte der Königlichen Sächsischen Gesellschaft der Wissenschaften. Mathematisch-Physische Klasse*, 20, 16–24.
- Horowitz, T., & Treisman, A. (1994). Attention and apparent motion. *Spatial Vision*, 8, 193–219.
- Julesz, B. (1971). *Foundations of cyclopean perception*. Chicago: University of Chicago Press.
- Krekelberg, B., & Lappe, M. (2001). Neuronal latencies and the position of moving objects. *Trends in Neuroscience*, 24, 335–339.
- Lotze, H. (1886). *Outline of psychology*. (G.T. Ladd, Trans). Boston: Ginn.
- Lu, Z., & Sperling, G. (1995). The functional architecture of human visual motion perception. *Vision Research*, 35, 2697–2772.
- Matin, L. (1972). Eye movements and perceived visual direction. In D. Jameson & L. M. Hurvich (Eds.), *Handbook of Sensory Physiology* (pp. 331–380). New York: Springer-Verlag.
- Müller, J. (1826). *Zur vergleichenden physiologie des gesichtsinnens*. Leipzig: Cnobloch.
- Nijhawan, R. (1994). Motion extrapolation in catching. *Nature*, 370, 256–257.
- Nijhawan, R. (2002). Neural delays, visual motion and the flash-lag effect. *Trends in Cognitive Science*, 6, 387–393.
- Ramachandran, V. S., & Anstis, S. M. (1983). Perceptual organization in moving patterns. *Nature*, 304, 529–531.
- Ramachandran, V. S., & Anstis, S. M. (1986). The perception of apparent motion. *Scientific American*, 254, 102–109.
- Ramachandran, V. S., & Anstis, S. M. (1990). Illusory displacement of equiluminous kinetic edges. *Perception*, 19, 611–616.
- Ross, J., Morrone, C., & Burr, D. C. (1997). Compression of visual space before saccades. *Nature*, 386, 598–601.
- Ross, J., Morrone, C., Goldberg, M. E., & Burr, D. C. (2001). Changes in visual perception at the time of saccades. *Trends in Neuroscience*, 24, 113–121.
- Schlag, J., Cai, R., Dorfman, A., Mohempour, A., & Schlag-Rey, M. (2000). Extrapolating movement without retinal motion. *Nature*, 203, 38–39.

- Schlag, J., & Schlag-Rey, M. (2002). Through the eye, slowly: delays and localization error in the visual system. *Nature Reviews Neuroscience*, 3, 191–200.
- Shioiri, S., Yamamoto, K., Kageyama, Y., & Yaguchi, H. (2002). Smooth shifts of visual attention. *Vision Research*, 42, 2811–2816.
- Suzuki, S., & Cavanagh, P. (1997). Focused attention distorts visual space: an attentional repulsion effect. *Journal of Experimental Psychology: Human Perception and Performance*, 23, 443–464.
- Ternus, J., (1938). The problem of phenomenal identity. In W. D. Ellis (Trans. and Ed.), *A source book of gestalt psychology* (pp. 149–160). London: Routledge & Kegan Paul.
- Verstraten, F. A. J., Cavanagh, P., & Labianca, A. (2000). Limits of attentive tracking reveal temporal properties of attention. *Vision Research*, 40, 3651–3664.
- von Helmholtz, H. (1962). *Helmholtz's Treatise on Physiological Optics*, vol. 3, (J.P.C. Southall Trans. and Ed.). New York: Dover (Original work published in 1866).
- Watanabe, K., Nijhawan, R., & Shimojo, S. (2002). Shifts in perceived position of flashed stimuli by illusory object motion. *Vision Research*, 42, 2645–2650.
- Watanabe, K., Sato, T. R., & Shimojo, S. (2003). Perceived shifts of flashed stimuli by visible and invisible object motion. *Perception*, 32, 545–559.
- Wertheimer, M. (1912). Experimentelle studien über das sehen von bewegung. *Zeitschrift für Psychologie*, 61, 161–165.
- Whitney, D. (2002). The influence of visual motion on perceived position. *Trends in Cognitive Science*, 6, 211–216.
- Whitney, D., & Cavanagh, P. (2000). Motion distorts visual space: shifting the perceived position of remote stationary object. *Nature Neuroscience*, 3, 954–959.
- Williams, Z. M., Elfar, J. C., Eskandar, E. M., Toth, L. J., & Assad, J. A. (2003). Parietal activity and the perceived direction of ambiguous apparent motion. *Nature Neuroscience*, 6, 616–623.