Voluntary attention modulates motion-induced mislocalization

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When a test is flashed on top of two superimposed, opposing motions, the perceived location of the test is shifted in opposite directions depending on which of the two motions is attended. Because the stimulus remains unchanged as attention switches from one motion to the other, the effect cannot be due to stimulus-driven, low-level motion. A control condition ruled out any contribution from possible attention-induced cyclotorsion of the eyes. This provides the strongest evidence to date for a role of attention in the perception of location, and establishes that what we attend to influences where we perceive objects to be.

Keywords: attention, perceptual organization, motion-2D

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Introduction

Whether capturing prey, avoiding predators, or catching a ball, it is essential to correctly see where things are located. But when an observer is moving or objects are moving, location must be computed on the basis of motion cues. This suggests that the processing of form, space and location is intimately related to the processing of motion. Indeed, there is evidence both that perceived motion is driven in part by form and spatial cues (e.g. Caplovitz, Hsieh, & Tse, 2006; Caplovitz & Tse, 2006, 2007, 2010; Hsieh & Tse, 2007; Lorenceau & Alais, 2001; McDermott, Weiss, & Adelson, 2001; Tse, 2006; Tse & Caplovitz, 2006; Tse & Logothetis, 2002; Wallach, 1935) and that perceived 3D form is driven in part by motion cues (Perotti, Todd, Lappin, & Phillips, 1998; Phillips & Todd, 1996; Siegel & Andersen, 1988, 1990; Todd & Norman, 2003; van Damme, Oosterhoff, & van de Grind, 1994) However, in certain circumstances, motion can induce the visual system to significantly misjudge shape or location so that an object is seen at a position where it is not actually present. For example, a circle can appear to be horizontally elongated if it suddenly replaces a vertically oriented ellipse (Suzuki & Cavanagh, 1998); an edge can appear displaced away from its true position when certain motion signals abut it (Anstis, 1989; Caplovitz, Paymer, & Tse, 2008; Ramachandran & Anstis, 1990), and a grating that drifts within a Gabor aperture can appear displaced because of the influence of motion signals on perceived position (De Valois & De Valois, 1991; Tse & Hsieh, 2006).

In general, motion can influence the perceived position of stationary objects (Whitney & Cavanagh, 2000) so that a briefly presented stationary object appears shifted in the direction of neighboring motion. This 'flash shift' effect allows us to examine a long-standing divide in the motion perception literature, where two different motion systems have been proposed. A low-level motion system (Anstis, 1980; Braddick, 1980; Cavanagh & Mather, 1989; Julesz, 1971) is thought to process velocity-based motion signals from the stimulus-driven responses of local motion detectors, while a high-level motion system (Cavanagh, 1992; Lu & Sperling, 1995; Seiffert & Cavanagh, 1998) is thought to process motion via object-token matching (Anstis, 1980) and attentional tracking of a target's position.

In the original report of the flash shift effect (Whitney & Cavanagh, 2000), both low-level and high-level motion systems may have contributed to object mislocalization because the stimulus was a sinusoidal luminance grating that could drive both systems. Subsequently, several papers have found evidence for a contribution from the high-level motion system to this position shift illusion in the absence of low-level motion energy. These studies used either motion viewed through apertures (Watanabe, Nijhawan, & Shimojo, 2002), inferred motion (Watanabe, Sato, & Shimojo, 2003), or apparent motion (Shim &

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Cavanagh, 2004; Whitney, 2006). Other studies have demonstrated the position shift for stimuli that could only drive the low-level motion system (Harp, Bressler, & Whitney, 2007; Whitney, 2005). One study presented the two motion levels in opposition by superimposing an equiluminous color grating rotating in one direction on top of a luminance grating rotating the other direction (Shim & Cavanagh, 2005). Under passive viewing the low-level motion of the luminance grating dominated. However, when subjects were asked to attentionally track a bar of the color grating and a test was briefly flashed near the superimposed gratings, the position of the test was shifted in the direction of the tracked, high level motion. These results showed that high-level, attention-based motion is sufficient to produce position shifts in the direction of attentional tracking even while low-level motion was moving in the opposite direction.

Here we go beyond this past work by demonstrating that an *identical* stimulus, composed of two rotating transparent layers, can lead to opposite perceived mis-localization, depending on how volitional attention is deployed to the stimulus under conditions of visual fixation. Because the stimulus remains unchanged as one attends first to one moving layer, and then the other, the effect cannot be due to the stimulus-driven low-level motion system. This provides the strongest evidence to date for a role of high-level motion processing and attention in the perception of location, and establishes beyond any doubt that what we attend to can influence where we perceive objects to be (Figure 1).

Methods and results

In our stimulus, two transparent layers are superimposed on a gray stationary field, one composed of transparent black, and the other of transparent white splotches. These transparent layers are rotated in opposite directions at a rapid angular velocity (290 angular degrees/second), then reverse direction after a fixed duration of 1200 ms, continually. Two vertically aligned solid red disks (diameter 4 visual degrees) appear for a very brief duration (~50 ms) on top of this motion stimulus upon the reversal of direction. In particular, the onset of the red disks occurs at the moment that the transparent white splotch layer starts rotating clockwise (CW) and the transparent black splotch layer starts rotating counterclockwise (CCW). Remarkably, the red spots are perceptually 'swept along' in the direction of the attended splotches' subsequent motion. This is an instance of motion assimilation (i.e., being swept in the direction of surrounding motion), not motion contrast (e.g., as occurs when the stationary moon appears to move in the

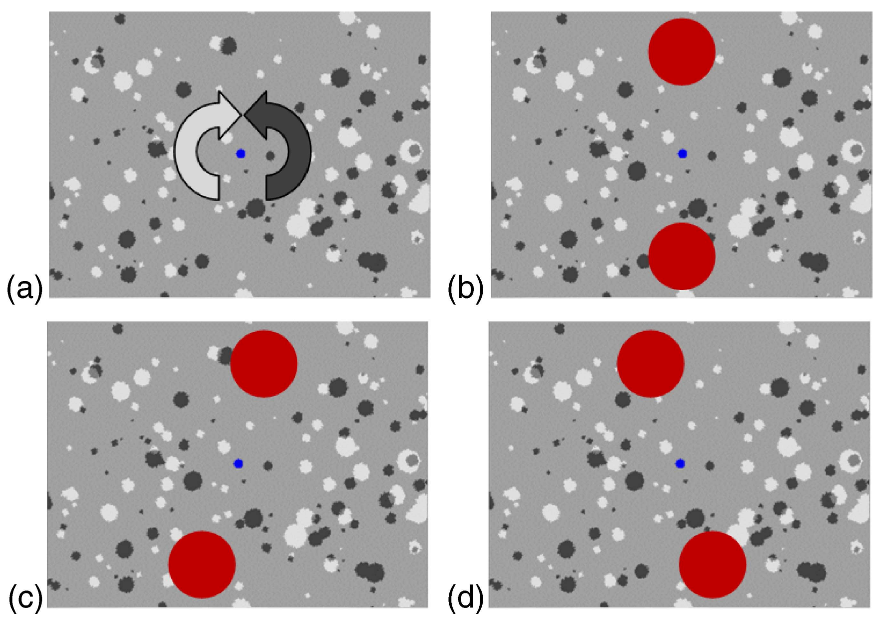
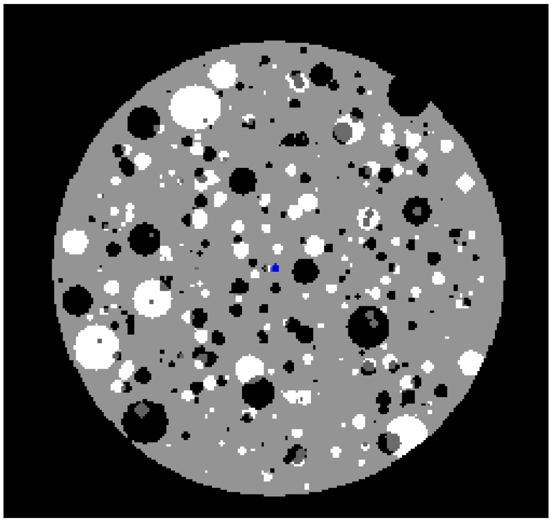


Figure 1. (a) Arrows indicate that the transparent layer that was composed of black splotches rotated in one direction, while the transparent layer that was composed of white splotches rotated in the opposite direction. Rotation direction reversed for both transparent layers simultaneously every 1200 ms. (b) The red disks were in fact always vertically aligned, and appeared for ~50 ms starting at the moment when the white transparent splotch layer began rotating CW and the black transparent splotch layer started rotating CCW. (c) When the white splotch layer was attended, the red disk pair appeared slanted to the right. (d) When the black splotch layer was attended, the red disk pair appeared slanted to the left.

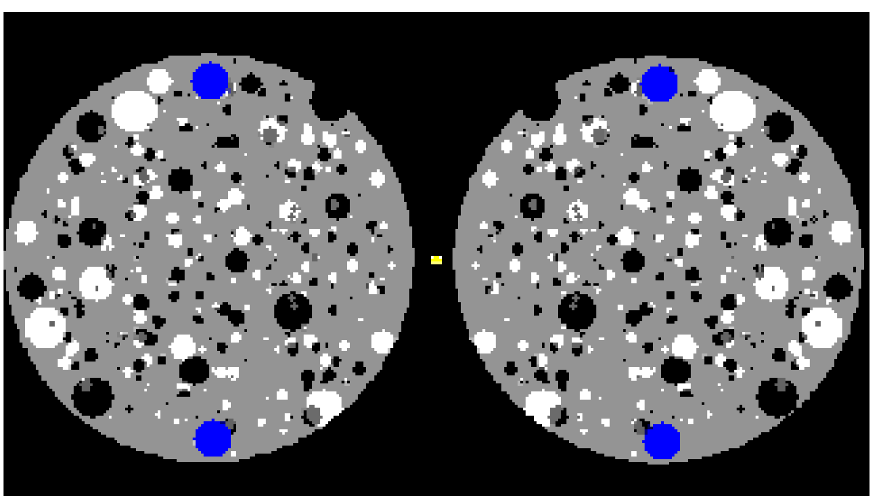


Movie 1. A demonstration of the basic attention-induced mislocalization effect. View all videos in loop mode. Fixate the blue central spot. When attending to the blue spot and not to either motion, the flashed red spots should appear to be aligned vertically, as they in fact are. However, while attending to the white (black) rotating layer and still fixating the blue dot, the red spot pair should appear slanted CW (CCW).

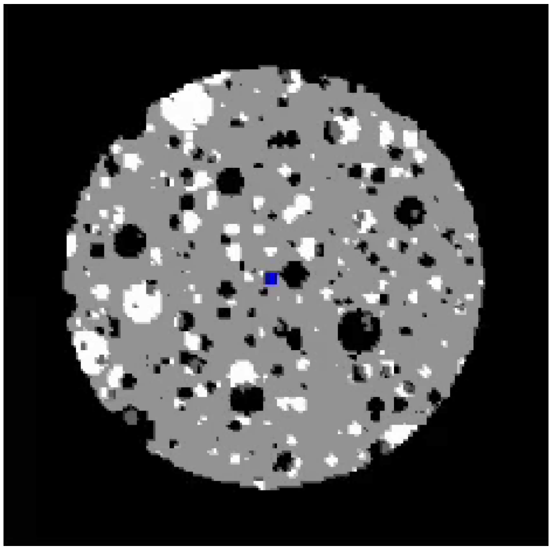
direction opposite the moving clouds). Thus when observers attend to the white splotches, the pair of red spots appears slanted CW, rather than CCW, because the red spots appear when the white layer starts to move CW.

Observers viewed the stimulus (30 visual degree disks spanning a 30 × 40 visual degrees Minolta Diamond gamma-corrected CRT monitor; red spot centers 12 degrees from fixation) from a distance of 57 cm while fixating the central blue fixation spot. They were either instructed to attend to the light or the dark splotch layer, and then report whether the red disk pair was slanted to the left (CCW) or to the right (CW) in a two alternative forced choice design. In particular, they were told to attend to an entire layer containing light (or dark) splotches, but not to try to attend to any particular individual splotches. Once fixation was ascertained, they initiated rotation of the stimuli by pressing a button. Subjects were not informed that the red dot pair was in fact vertically aligned. They were permitted to view the stimulus for as many cycles of red spot appearance as they wished. All sixteen observers who were instructed to attend to the transparent white dot layer reported that the red dot pair appeared slanted to the right (CW), while fourteen of sixteen observers who were instructed to attend to the transparent black dot layer reported that the dot pair appeared slanted to the left (CCW; binomial test, p < 0.0001 in both cases). A demonstration of the stimulus can be viewed in Movie 1. A more elaborate variant can be seen in Movie 2. The effect is very robust, and works well using many combinations of colors, luminances, sizes, and speeds, as long as there are two oppositely moving transparent layers, and as long as the spots appear at the moment of the motion reversal.

To control for the possibility that attending to a given motion layer might induce cyclotorsional eye movements that could account for the apparent rotation of the red dot pair, a control experiment was performed where, in addition to the same pair of red spots as before, there now



Movie 2. In this variant of the basic effect, fixation is maintained between two counterphase rotating transparent layers. If the white layer on both sides is attended, the blue pair of dots on the left (right) should appear rotated CW (CCW; rather like a “V”) and the red pair on the left (right) should appear rotated CCW (CW; rather like an upside down “V”). In contrast, if the black layer on both sides is attended, the blue pair on the left (right) should appear rotated CCW (CW; rather like an upside down “V”) and the red pair on the left (right) should appear rotated CW (CCW; rather like a “V”).



Movie 3. In order to control for the possibility that mislocalization is due to attention-induced cyclotorsional eye movements, a control condition, demonstrated here, was carried out in which vertical bars appear at the same time as the flashed red spots but at more eccentric locations. The cyclotorsion account predicts that the bars and dots should lie on a slanted virtual line. In fact the red spots undergo the position shift illusion, while the bars do not, ruling out cyclotorsion as the cause of the illusion.

appeared, at the exact same time as the red spots, and for the same duration, two vertically aligned bars outside the moving transparent surfaces. Cyclotorsional eye movements would predict that the two vertical bars would be even further displaced from vertical than the red spots, and in the same direction. In effect, any attention-induced rotation of the eyeball should make the red spots and bars fall on a single slanted line. However, if motion-induced displacement is not due to cyclotorsional eye movements, the displacement should be smaller for the bars than the red spots because motion-induced displacement decreases in magnitude with distance from the moving source (Durant & Johnston, 2004). In this case, regardless of which layer was attended, no motion-induced displacement was reported in the vertically aligned bars by any observer ($n = 7$; binomial test $p < 0.01$), even when motion-induced displacement was observed for the red dots. If the effect were due to attention-induced rotation of the eyeball, the red dots should appear misaligned. Because they are not misaligned from vertical, the effect cannot be due to this possible confounding factor. A demonstration of this control can be seen in Movie 3.

Discussion

These results demonstrate that the motion-induced position shift can be generated as a consequence of the attended motion direction alone. We can rule out cyclotorsion or low-level motion energy, which is balanced in our stimuli, as the cause of the effect. These results go beyond previous findings concerning the role of attention in position mislocalization (Shim & Cavanagh, 2004, 2005; Suzuki & Cavanagh, 1997; Watanabe et al., 2002, 2003; Whitney, 2006), by showing that the same stimulus can have an effect in either direction depending on which direction is attended.

What can account for this remarkable effect of attention on perceived position? When subjects select one of the two moving surfaces, the position shift is appropriate to the selected motion. Since the low-level motion of the two transparent surfaces is equal in both directions, the robust displacement must be due to the attended motion, consistent with the result of Shim and Cavanagh (2005) who showed that high-level motion determines the motion-induced position shift even when low-level motion is present in the opposite direction. Demonstrating that the attended motion alone is sufficient to shift a test flash does not, however, explain the shift. Some have proposed that the perceived position of moving targets is extrapolated to compensate for neural delays (Nijhawan, 1994) or to provide for appropriate reach (Whitney, 2008) or saccade targeting (de'Sperati & Baud-Bovy, 2008; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011), although there is evidence against extrapolation for purposes of compensation (see Eagleman & Sejnowski, 2007, for a review). Whatever the reason, it is clear that moving targets are extrapolated, being shifted even into the blind spot (Cai & Cavanagh, 2002; Maus & Nijhawan, 2008). However, the issue with the flashed dots in our experiments and others since Whitney and Cavanagh (2000) is that the test dots are not moving and yet they appear shifted. It has been suggested that the test flashes are captured by the moving stimulus and are assigned a motion. However, although they appear shifted, they do not subjectively appear to be in motion (Whitney & Cavanagh, 2003). Moreover, the shift effect is strongest if the dots are flashed briefly at the moment of motion reversal (Whitney & Cavanagh, 2000) whereas there is little or no perceived shift if they are flashed briefly more than 500 msec before or after a reversal. There therefore appear to be at least three necessary conditions for the occurrence of the flash shift effect: First, the to-be-mislocalized objects (here red dots) must be presented very briefly, on the order of 50 ms; Second, there must be motion in the neighborhood of the dots; And third they should be presented at the moment of a motion reversal. Why this is so is not yet understood. Possibly, the motion uncertainty at the moment of reversal allows the new motion direction, namely, the direction following the reversal, to be briefly assigned to the flash, which itself has ambiguous motion, balanced in strength in all directions. These results do not solve the as yet unsolved riddle of the source of the perceived displacement, but they do demonstrate that once the above necessary conditions are met, attentional allocation is sufficient to drive the displacement in opposite directions when two oppositely moving overlapping transparent layers are present. This implies that perceived location can be driven in part by volitional allocation of attention and provides further evidence that focused attention can distort the encoding of nearby positions (Suzuki & Cavanagh, 1997). This suggests that the 'binding' of features such as redness and roundness to perceived locations is not independent of the encoding of attention within a spatial map of salient and attended locations (Cavanagh, Hunt, Afraz, & Rolfs, 2010).

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