



Motion-induced position shifts are influenced by global motion, but dominated by component motion



Peter J. Kohler^{a,*}, Patrick Cavanagh^b, Peter U. Tse^c

^a Department of Psychology, Stanford University, 450 Serra Mall, Stanford, CA 94305, United States

^b Laboratoire Psychologie de la Perception, Université Paris Descartes, Sorbonne Paris Cité, and CNRS UMR 8242, 75006 Paris, France

^c Department of Psychological & Brain Sciences, Dartmouth College, 6207 Moore Hall, Hanover, NH 03755, United States

ARTICLE INFO

Article history:

Received 15 October 2014

Received in revised form 27 February 2015

Available online 14 March 2015

Keywords:

Motion-induced position shifts

Component motion

Global motion

ABSTRACT

Object motion and position have long been thought to involve largely independent visual computations. However, the motion-induced position shift (Eagleman & Sejnowski, 2007) shows that the perceived position of a briefly presented static object can be influenced by nearby moving contours. Here we combine a particularly strong example of this illusion with a bistable global motion stimulus to compare the relative effects of global and component motion on the shift in perceived position. We used a horizontally oscillating diamond (Lorenceau & Shiffrar, 1992) that produces two possible global directions (left and right when fully visible versus up and down when vertices are occluded by vertical bars) as well as the oblique component motion orthogonal to each contour. To measure the motion-induced shift we flashed a test dot on the contour as the diamond reversed direction (Cavanagh & Anstis, 2013). Although the global motion had a highly significant influence on the direction and size of the motion-induced position shift, the perceived displacement of the probe was closer to the direction of the component motion. These findings show that while global motion can clearly influence position shifts, it is the component motion that dominates in setting the position shift. This is true even though the perceived motion is in the global direction and the component motion is not consciously experienced. This suggests that perceived position is influenced by motion signals that arise earlier in time or earlier in processing compared to the stage at which the conscious experience of motion is determined.

© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

The earliest demonstration of an interaction between motion and position encoding was probably Fröhlich's (1923) discovery that the starting position of a moving object appeared to be shifted along the motion trajectory. More than 70 years later, Nijhawan (1994) expanded on earlier observations by Mackay (1958), and showed that a briefly presented, stationary stimulus is perceived as lagging behind a moving stimulus, although they are physically aligned (the flash lag effect; Nijhawan, 1994). Two other groups reported that even when the stimulus itself did not move, the motion of a texture inside it shifted the perceived position of the stimulus (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990). Moreover, if the stimulus with the internal motion then actually does move, the perceived trajectory deviates strongly from the physical trajectory (the infinite regress illusion; Tse & Hsieh,

2006). Two further versions use a briefly presented “flash” stimulus, one in which the flash is presented adjacent to a moving stimulus (the flash drag effect; Whitney & Cavanagh, 2000) and one in which the flash occurs on the moving stimulus itself (the flash jump effect; Cai & Schlag, 2001a; Cai & Schlag, 2001b; Sundberg, Fallah, & Reynolds, 2006). In both cases, the flash is seen displaced in the direction of the motion.

In recent years, several important advances have been made towards understanding how and why these illusions occur, and many of them may in fact be caused by the same underlying mechanism (Eagleman & Sejnowski, 2007). In the experiments reported here we focus on a specific aspect of the illusions that is still not well understood, namely the exact nature of the motion signals driving the position shifts. We use a particularly strong motion-induced position shift that has been called the “flash grab effect” (Cavanagh & Anstis, 2013). This effect occurs when a moving stimulus undergoes a direction reversal, and a flash is briefly presented at the same time and position as the reversal. The flash is strongly shifted in the direction of motion after the reversal. This perceived shift can be up to 10 times larger than the flash drag

* Corresponding author.

E-mail addresses: pjkohler@stanford.edu (P.J. Kohler), patrick.cavanagh@paris-descartes.fr (P. Cavanagh), peter.u.tse@dartmouth.edu (P.U. Tse).

effect, up to several times the physical size of the flash and several degrees of visual angle (Cavanagh & Anstis, 2013).

Several studies have shown that motion-induced position shifts do not require low-level motion that drives early, direction-selective neurons (Hubel & Wiesel, 1962), but can also be generated by high-level motion and global motion. High-level motion refers to stimuli that are seen to move even though they do not drive early motion-selective units. These stimuli either have no net motion of luminance-defined features (e.g., motion of texture-defined contours; Cavanagh & Mather, 1989) or their luminance features jump too far to stimulate low-level detectors (Anstis & Mackay, 1980). Global motion refers to the direction that an object is seen to move even though many or all of its constituent contours have component motion directions (the directions orthogonal to each local contour) that are very different (Nakayama & Silverman, 1988).

Several reports have shown that position shifts are not driven solely by local, image-level motion signals. A pattern containing global motion (plaids or dynamic Gabor arrays) produced shifts corresponding to the global direction rather than the two local component directions (Hisakata & Murakami, 2009; Mather & Pavan, 2009; Rider, McOwan, & Johnston, 2009). Similarly, two studies have demonstrated that shifts can be driven by second-order motion (Bressler & Whitney, 2006; Pavan & Mather, 2008). Position shifts can also be induced by high-level motion signals generated during anorthoscopic perception (Watanabe, Nijhawan, & Shimojo, 2002) and by objects moving behind an occluder (Watanabe, Sato, & Shimojo, 2003) in the near-absence of low-level motion signals. The flash drag effect can even be elicited along the perceived motion path (Shim & Cavanagh, 2004) with a bistable apparent motion quartet stimulus, where there is no net motion energy in the image. Furthermore, a recent study using the flash grab effect found that when one of two overlapping transparent surfaces moving in opposite directions is attended, the flash grab effect will correspond to the attended surface (Tse et al., 2011) even though the two low-level motion signals are equal and opposite in direction. Even implied motion, induced by static photographs, can lead to a flash drag effect (Pavan et al., 2011).

These previous studies focused on demonstrating an effect of global or high-level object motion that was different from what would be expected based on purely local component motion signals, especially when component motion signals were absent or nulled. Here we examine what happens when both component and global motion signals are available. We wanted to determine the extent to which global and component motion contribute to the shift, by pitting the two types of motion against one another in the same stimulus. If motion-induced position shifts are not influenced by component motion whatsoever, shifts in perceived position should follow the global motion direction.

Our stimulus was created by combining a well-known bistable moving diamond stimulus (Lorenceau & Shiffrar, 1992) with the flash grab effect. We presented two diamonds that moved horizontally back and forth across the screen under conditions that induced differences in perceived motion direction (see Fig. 1A–B). According to Lorenceau and Shiffrar (1992), when the diamonds are shown without occlusion, or with visible occluders, the diamonds appear to move horizontally. When the occluders are the same color as the background, however, the diamond line segments appear to move vertically and independently, presumably because terminator motion measured at the line end-points dominates the conscious motion percept (McDermott, Weiss, & Adelson, 2001). Importantly, although these conditions produced very different global motion percepts, the component motion along the line segments at the position where the motion-induced position shift was to be tested was always identical and orthogonal to the orientation of the line.

To test the position shift, a dot probe was flashed in the middle of the line segment at the time of each motion reversal (see Fig. 1A). The two diamonds alternately reached the same reversal position and the probe was flashed at that same physical location. Depending on which diamond was moving, the probe was either red or blue. Since the two diamonds moved away from the probe location in opposite directions, the red and blue probes were shifted in opposite directions, doubling the size of the effect (see Fig. 1C). To report the position shift, participants adjusted a pair of dots to mimic the direction and distance of the offset they saw between the two colored dots. This resulted in a highly robust, basic position-shift effect with a motion stimulus that was seen with one of two different global motion directions, without any difference in component motion signals at the flash location.

2. Methods

Six participants (3 males; ages 18–23, mean age = 20.4) took part in a control experiment that measured motion direction. Eleven additional participants (5 males; ages 19–23, mean age = 20.4) took part in the main experiment, which measured position shift direction. All were members of the Dartmouth College community with normal or corrected to normal vision, who volunteered to participate. Each participant gave written informed consent prior to the experiment according to the guidelines of the IRB and Department of Psychology at Dartmouth College. All were naïve to the purpose of the experiment, and received \$10/h in compensation.

Participants viewed the visual stimulus from a distance of 57 cm, in a darkened room, constrained by a chin rest. The stimuli were presented on a Mitsubishi Diamond Pro 2070SB CRT monitor (1600 × 1200 pixels, at a 60 Hz refresh rate), and generated using the Psychophysics Toolbox, version 3, on a PC running MATLAB R2010a (Brainard, 1997; Pelli, 1997) in an Ubuntu Linux operation system.

Three versions of the oscillating diamond stimulus were used. In the “complete diamond” version, the diamonds were shown without occlusion, which, according to Lorenceau and Shiffrar (1992), leads to an unambiguous percept of a diamond moving back and forth horizontally (see Fig. 1B). In the “line segment” version, the diamond moved left and right horizontally while its vertices were occluded by three vertical bars that had the same color as the background (see Fig. 1B). In this version, the line segments are often seen in independent vertical motion (Lorenceau and Shiffrar (1992), entrained by the vertical terminator motion measured at visible line segments endpoints (McDermott, Weiss, & Adelson, 2001). Finally, in the “outline occluders” condition, a thin yellow outline was added to all the occluder regions to make them appear visible and separate from the background. Lorenceau and Shiffrar (1992) reported that the horizontal motion of the diamond was seen once again in this case because the visible occluders “explained” the vertical terminator motion by making those terminators extrinsic to (i.e. not belonging to) the moving line segments.

To test the extent to which these three versions of the diamond stimulus could produce the expected motion percepts, a perceptual control experiment was run in which participants indicated the motion direction that they perceived for each of the three versions by rotating a dumbbell indicator to align it with the perceived direction. A fixation cross (0.81° vis. angle in width and height) was presented in the center of the screen. We used two diamond stimuli (height: 19.2° vis. angle, width: 28.8° vis. angle) that moved in an interleaved fashion (two diamonds were used to double the size of the position shift in the main experiment from what would be elicited by a single diamond). One diamond was centered at a starting position ~4.1° vis. angle to the left of fixation, and another

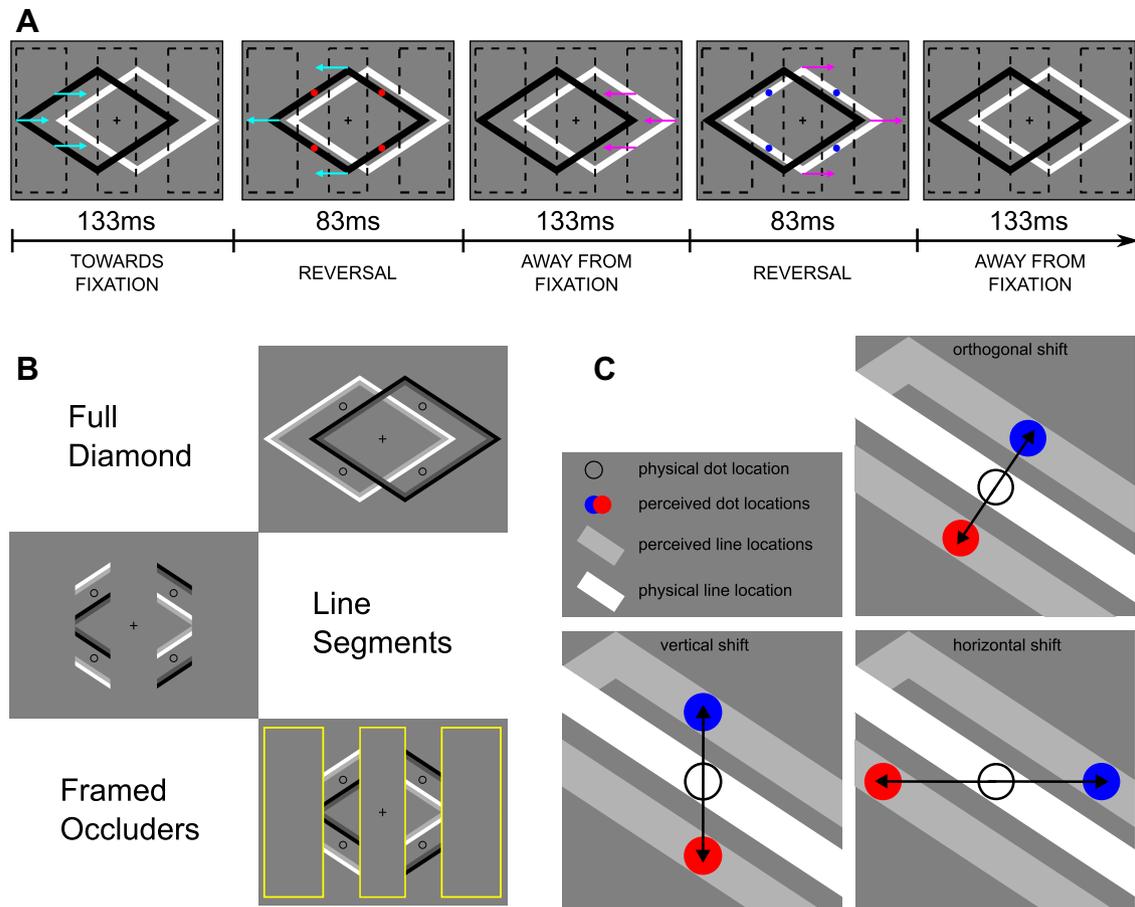


Fig. 1. *Stimulus.* (A) A single cycle of the stimulus in the main experiment. The two diamonds moved one at a time, and paused for 83 ms at reversal while a single dot was presented, red or blue depending on which diamond was moving. This caused the dot to appear to be shifted in opposite directions at the two presentation locations, and the dot color was varied to make it easier for participants to perceive the effect. The motion paths of the two diamonds are illustrated with pink and cyan arrows. Dots were always presented in the same location, in one of the four quadrants. The same stimulus was used in the control experiment, except that no dots were presented. (B) The three experimental conditions. Only the occluders differed between conditions, and they were either not presented at all (“Full Diamond”), presented in the same color as the background (“Line Segments”) or presented in the same color as the background with a yellow border outline (“Framed Occluders”). (C) Examples of three canonical shift directions, exaggerated for illustration. Outline dot represents physical dot position, while red and blue dots represent the shifted, perceived position for red and blue dots, respectively. The physical diamond position at reversal is indicated with a thick white line, while the two thick gray lines indicate the perceived reversal point of each diamond, shifted in opposite directions by the motion. Note that for simplicity, the occluders are not shown on this figure. Participants adjusted a dumb-bell on a separate screen to indicate the shift direction. Demo videos of the 3 conditions are included as [Supplementary Material](#). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

was centered at the same distance to the right of fixation. To make the diamonds as distinguishable as possible, and at the same time maximize the diamond outline contrast, one diamond outline was white and light gray, while the other was black and dark gray (total line width: 1.6° vis. angle, see Fig. 1B). Each diamond moved horizontally toward fixation at a speed of 30.4° vis. angle/sec until it was centered on fixation, and then reversed direction and returned to its starting position, where it remained while the other diamond was moving. At each reversal the diamond remained stationary for five monitor refresh frames (~ 83 ms).

Participants initiated each trial by pressing the space key, at which point the diamonds appeared and began their interleaved left/right motion. Participants were instructed to fixate the central fixation cross while covertly directing their attention to the moving contours. Fixation was monitored using an SR Research EyeLink2 head-mounted eye-tracker. If the point of fixation strayed more than 2° away from central fixation while the moving stimulus was displayed, the stimulus was replaced by a blank screen and the trial was suspended until central fixation had been re-established. When participants pressed the space key the moving

stimulus was removed from the screen and replaced by a dumbbell consisting of two black dots connected by a line. On each trial the dumbbell was shown in one of four locations on the screen, corresponding to the reversal points of the four diamond line segments (and to the dot probe locations in the main experiment, see below).

Participants used the left and right arrow keys to adjust the dumbbell such that it matched the perceived motion direction (see Fig. 1C). Participants had unlimited time to inspect the test stimulus, and were instructed to switch back and forth between the test and the adjustment screen until they were satisfied that the dumbbell matched their percept of the motion direction as closely as possible. At this point they pressed the enter key to advance to the next trial. In order to encourage participants to pay attention to the display as a whole, the dumbbell was shown 5 times at each of the four locations, for all three conditions. This added up to a total of 60 trials per participant, which were presented in random order.

In the main experiment the goal was to measure the angle and magnitude of the position shift induced by the diamond motion.

The stimulus was identical to the motion direction control experiment with the following changes. First, we presented a circular dot probe (diameter: 1.1° of visual angle) on top of one of the four diamond line segments, halfway between the occluders (see Fig. 1A) at a location 4.5° from the fixation. This meant that on each trial the dot probe could be presented in one of four possible locations, offset obliquely from fixation. The dot probe then became subject to the flash grab effect – the end positions of the two diamonds were identical so the dot was always presented at the same location within each trial, but because the two diamonds were moving in opposite directions, perceptually the dot was shifted in opposite directions, depending on which diamond was moving (see Fig. 1C). In order for participants to clearly see and report the effect, the dot probe was shown in either red or blue, depending on which diamond was moving. Second, the procedure and eye monitoring were the same as in the perceptual control except that participants were now instructed to covertly direct their attention to the flashing red and blue dot probes, while fixating the central fixation cross. When participants pressed the space key the moving stimulus was removed from the screen and replaced by a dumbbell at the dot probe location, identical to the one used in the control experiment. Participants used the arrow keys to adjust the dumbbell such that it matched the perceived angle (left and right keys) as well as distance (up and down keys) between the red and blue dot on the other screen (see Fig. 1C). The trials were repeated 5 times with dot probes and dumbbells at each of the four locations, for all three conditions. This added up to a total of 60 trials per participant, which were presented in random order.

3. Results

The same procedure was followed for both the main experiment and the control experiment: We computed the angle and distance

between the two dots, reported in each trial by each participant. We then computed a within-participant average of both angle and speed for each quadrant (within-participant averages, averaged across the four quadrants, are plotted as vectors in Fig. 2A). The data from the main experiment showed that while all three versions of the stimulus had a strong motion-induced position shift, the shift angle and magnitude differed across stimuli. We analyzed this by computing the within-participant average reported angle and distance between the red and blue dot for each quadrant and performing a two-way repeated measures ANOVA with condition as the first level and quadrant (the four different test locations) as the second level, on both measures. For the shift angle there was a significant main effect of condition ($F(10,2) = 24.3$, $p < 0.001$), no effect of quadrant ($F(10,3) = 2.43$, $p = 0.085$) and no interaction ($F(10,6) = 1.22$, $p = 0.336$). For the shift magnitude (i.e. the reported distance between the dots), there was also a significant main effect of condition ($F(10,2) = 11.47$, $p < 0.001$), and again no effect of quadrant ($F(10,3) = 0.25$, $p = 0.86$) and no interaction ($F(10,6) = 0.77$, $p = 0.59$). This result indicates that our experimental conditions had strong effects on both the direction and size of the motion-induced shift. As expected, the quadrant in which the dot probe was located had no effect on the motion-induced position shifts, and we will not consider the quadrant variable any further.

To compare each of the three main experiment conditions directly, we averaged each participant's reported shift angles and magnitudes for each condition across the quadrants. The within-participant cross-quadrant averages are plotted as vectors in Fig. 2A, with the overall averages of the same data shown in Fig. 2B. We then performed paired t -tests between the conditions: The complete diamond condition had a significantly smaller angle than both the line segment condition ($t(10) = 5.55$, $p < 0.001$) and the outlined occluders condition ($t(10) = 4.13$, $p < 0.005$),

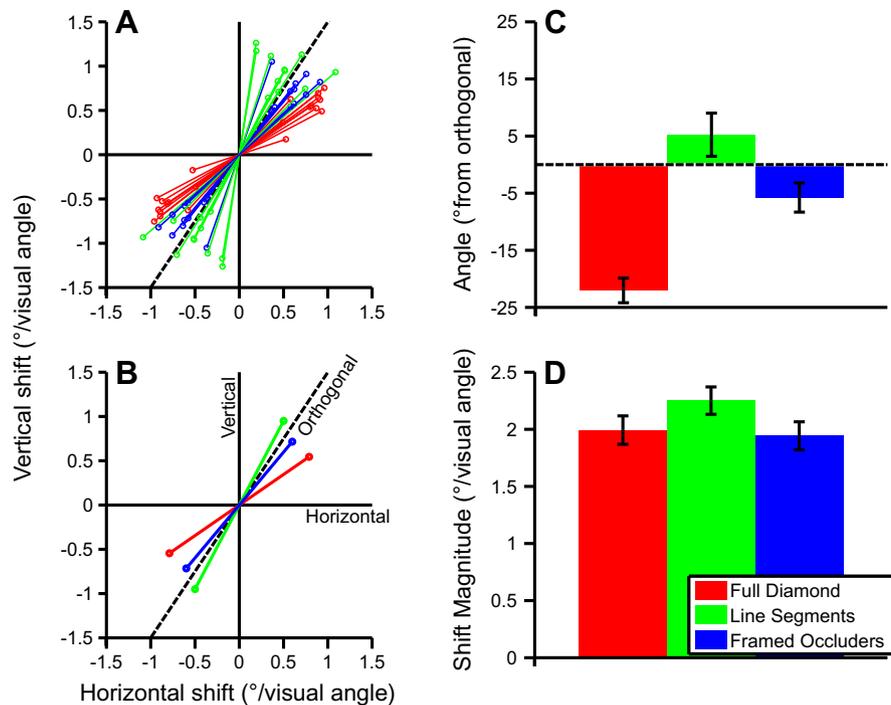


Fig. 2. Results of the main experiment. The left side of the figure shows shift angle and distance averaged across quadrants, and plotted as vectors. (A) Within-participant averages, each line indicates the response of a single participant to a specific experiment condition. (B) Grand means across participants. The dotted lines on plot A and B indicates the angle consistent with an orthogonal shift, the vertical line indicates the angle consistent with a vertical shift, and the horizontal line indicates the angle consistent with a horizontal shift. The right side of the figure shows the average shift angle (C; units are $^\circ$ of rotation off orthogonal) and shift distance (D; units are $^\circ$ of visual angle), plotted separately as bar plots. On the angle plot, the dotted line again indicates the orthogonal angle. Negative values indicate a more horizontal shift, while positive values indicate a more vertical shift.

indicating that the complete diamond led to a more horizontal shift than the other two conditions (means and standard errors of the shift angles are shown as bar plots in Fig. 2C). We also found a significant difference between the line segment and outlined occluders condition ($t(10) = 4.20, p < 0.005$), indicating that outlined occluders led to a more horizontal shift than line segments. Equivalent paired t -tests for the shift magnitude indicated that the line segment condition led to a bigger shift than either the complete diamond ($t(10) = 4.12, p < 0.005$) or the outlined occluders condition ($t(10) = 4.15, p < 0.005$), and that the magnitude between these two conditions did not significantly differ ($t(10) = 0.49, p > 0.05$; means and standard errors of the shift magnitudes are shown as bar plots in Fig. 2D).

As expected, the motion direction control experiment showed that the full diamond version of the stimulus was perceived as moving horizontally by all participants (average motion direction, where zero is horizontal: $0.7^\circ \pm 1.0^\circ$). In the line segment condition, the lines were seen to move almost vertically (average: $76.5^\circ \pm 11.7^\circ$), with only a single participant judging their direction as more than 10° different from vertical. On the other hand, the perceived motion direction for the outlined occluder condition was also closer to vertical than horizontal (average: $67.0 \pm 13.5^\circ$). This indicates that although the full diamond and line segment conditions consistently evoked the horizontal and vertical global motion percepts that we had expected, our outlined occluder condition did not yield the expected horizontal global motion percept. Recall that all of these three versions have the same component motion directions, orthogonal to the contours (so 56.3°) regardless of the direction of the global motion percept.

4. Discussion

Our double diamond stimulus evoked a large motion-induced position shift with a magnitude of about 1° of visual angle at 4.5° eccentricity. More importantly, our results corroborate previous findings that global motion signals can influence perceived position. The component motion at the location where the probes were presented was the same in all three conditions, yet the direction of the position shift was more horizontal for conditions that were biased toward horizontal global motion, and more vertical for the condition that was biased toward vertical global motion. Local component motion detectors can only read out signals that are orthogonal to the angle of the moving edge (Nakayama & Silverman, 1988). Because of this, we can use the shift angle's deviation from orthogonal (56.3° for our diamond; see Fig. 1C) as a measure of how much influence global motion had on the motion-induced position shift (the orthogonal angle is shown with a dotted line in Fig. 2A–C). The mean shift angle deviation from orthogonal was $\sim 22^\circ$ toward horizontal for the complete diamond, and $\sim 6^\circ$ toward horizontal for the outlined occluders condition. That the outlined occluders condition produced a weaker effect is not surprising, because the motion direction control experiment showed that this condition failed to consistently evoke a horizontal motion direction percept. As expected, the line segment condition deviated in the opposite direction of the other two conditions, toward vertical, and this deviation was $\sim 5^\circ$ from orthogonal, again smaller than what was seen for the full diamond condition.

We can derive the relative contribution of the component and global motion vectors across our 3 stimulus conditions by computing the regression line between perceived motion direction (as measured in the control experiment) and the motion-induced shift direction (as measured in the main experiment), with both values expressed as the deviation from the direction orthogonal to the contour orientation at the test location. The slope of the regression model is equivalent to the relative contribution of global motion to

the shift direction: a slope of 0 indicates that only local motion determines the motion-induced shift direction whereas a slope around 1 indicates that only global motion influences the perceived shift direction. We computed slope values using the shift direction values from each participant in our main experiment combined with the mean motion direction values from the control experiment. Our data yield a mean slope value of 0.32 ± 0.20 , which is significantly larger than 0 (right-sided t -test: $t(10) = 5.24, p < 0.001$), indicating that the motion-induced shift direction was not completely determined by local, component motion. The slope is, however, also significantly smaller than 1 (left sided t -test: $t(10) = 11.25, p < 0.001$), indicating that the shift direction was not completely determined by the global motion. The relatively low value of slope (less than 0.5) shows that while global motion indeed has an influence on the direction of motion-induced shift, the perceived shift direction was dominated by component motion. Importantly, this was the case even though participants did not consciously experience the component motion. To our knowledge, such a discrepancy between position shifts and global motion has not been demonstrated previously. The closest precedent is a study by Pavan and Mather (2008), in which first- and second-order motion stimuli presented within a stationary window were found to have independent, non-interacting effects on the perceived position of the window. The authors concluded that first- and second-order motion systems were independently interacting with position encoding (Pavan & Mather, 2008).

A potential explanation of the weak effect of global motion direction on the motion-induced position shift is the possibility of bistability in the global motion percept (which might sometimes be seen as horizontal, sometimes vertical). Averaged across trials, this would move the mean perceived direction away from the two global directions, toward the local direction (just because it lies between the two global directions). If the direction of the position shift reported in the main experiment followed the trial-to-trial variability in global motion direction, its averaged direction would also appear to be a better match to the component motion (orthogonal to the moving contour). Importantly, this is not the case. The perceived motion judgments showed weak bimodality across trials only for the framed occluder condition, an effect which did move the mean perceived direction toward the oblique (see Supplementary Materials). However, the motion-induced position shifts showed no evidence of bimodality across trials in any of the conditions including the framed occlude condition. We conclude that it is unlikely that we underestimate the contribution of global motion due to bimodal response distributions: even the weak bimodality in one perceived motion direction condition was not passed on to the motion-induced position shifts.

Although the stimulus was removed from the screen whenever participants moved their eyes more than 2° of visual angle away from fixation, eye-movements may still have had an influence on the position shift results. Systematic differences in the eye movements of fixation between the three conditions could potentially lead to differences in the position shift direction (Rolfes, 2009). To assess whether eye movements could have had an influence on our results, we analyzed the eye movements of fixation made by participants during the experiment (see Supplementary Materials). This analysis indicated that eye movements were not significantly correlated with position shifts, and not different among conditions overall, so we conclude that eye movements are unlikely to have influenced our position shift results.

In addition to the differences in position shift angle between the different conditions, we also found a difference in the magnitude of the position shift, such that the line segment condition (mean shift magnitude 2.25° vis. angle) elicited a 12.5% bigger shift than both the full diamond and the outlined occluders (mean shift magnitude for both: $\sim 2^\circ$ vis. angle). We can speculate about why this might

occur – perhaps the terminator signals at the line ends that drive the vertical motion percept yield a stronger, less ambiguous motion signal than the one elicited by integration of motion over the entire diamond. This explanation is somewhat contradicted by the finding that horizontal global motion had a stronger effect on the perceived shift direction than vertical motion. Another possibility is that there is a difference in perceived speed between the line segment and diamond percepts. We have previously shown that motion-based grouping can lead to a 10–15% decrease in perceived speed (Kohler, Caplovitz, & Tse, 2009; Kohler, Caplovitz & Tse, 2014), and grouping the four line segments into a coherently moving diamond could have a similar effect. Cavanagh and Anstis (2013) have found that the size of the position shift increases with speed until it saturates at about 41.2° vis. angle/second (270° of rotation/second in their experiment; see Cavanagh & Anstis, 2013). Our stimulus speed (30.4° vis. angle/second) was below that saturation level, so differences in perceived speed due to perceptual grouping could potentially explain the smaller position shift for the diamond percept.

The relative contributions of different motion types to the motion-induced position shift can reveal the level of visual processing at which the shift in position emerges (McGraw, Walsh, & Barrett, 2004). If non-local motion signals can contribute to shifts in perceived position, it suggests that the interaction between motion and position must occur in areas late in the visual processing stream, where these non-local motion signals are encoded. The middle temporal area of visual cortex (MT) is a key area for motion perception. In monkeys, MT neurons have been shown to contribute importantly to perceived motion (Salzman, Britten, & Newsome, 1990) and have tuning functions that match psychophysical data very well (Britten et al., 1992). fMRI work on the human homologue of MT (hMT+), indicates that this area is strongly selective for motion direction, more so than areas earlier in the visual processing stream (Huk, Ress, & Heeger, 2001). Importantly, hMT+ has also been found to encode many higher-level motion percepts, including integration of component motion signals into global motion (Born, Tsui, & Pack, 2010; Mather & Pavan, 2009; Pack & Born, 2001), anorthoscopic perception (Yin et al., 2002), apparent motion (Muckli et al., 2002; Sterzer, Haynes, & Rees, 2006), and implied motion (Kourtzi & Kanwisher, 2000). Given the psychophysical data demonstrating that each of these non-local motion signals can contribute to position shifts, hMT+ would appear to be a strong candidate area for encoding motion-induced position shifts. This hypothesis is supported by fMRI data showing that hMT+ is capable of representing perceived object position at a very fine-scale (1/3°/visual angle or less; Fischer, Spotswood, & Whitney, 2011), and by several experiments using TMS (Maus et al., 2013; McGraw et al., 2004), and fMRI (Maus, Fischer, & Whitney, 2013), all finding evidence that hMT+ represents motion-induced position shifts. This means that a simple model could be proposed in which both perceived position and non-local motion are resolved in hMT+, based on inputs from areas earlier in the visual processing stream.

Our results do not contradict the hypothesis that hMT+ is important for representing perceived position, and indeed support it in that as we also find that global motion can influence motion-induced position shifts. However, our finding that the position shift is not determined solely by the global motion percept and can deviate substantially from the consciously perceived, global direction of motion does pose some challenges for a simple model of motion-induced position shifts. Our result that local component motion plays a strong role in the position shift can be interpreted in at least two ways. The first explanation proposes that perceived position is influenced by processing at multiple stages in the visual system, and that the influence of component motion occurs outside of hMT+. If position is partially encoded at stages of visual

processing where component motion signals are more prevalent than global motion signals, it may lead to the effects we see. While MT neurons are sensitive to global motion (Pack & Born, 2001), V1 neurons have been shown to respond to local stimulus features like contours and also terminators (Pack, Gartland, & Born, 2004). In the line segment condition of our experiment, the vertically moving terminators are 3.37° of visual angle from the dot center, and in the full diamond condition the diamond vertices are at an even greater distance from the dot. So even taking into account the dot radius (0.55° of visual angle), it is unlikely that V1 receptive fields at the physical dot position would extend to capture the terminator motion (Pack, Gartland, & Born, 2004). Instead, these receptive fields are likely to exclusively capture local contour information, which means that the local motion component of the motion-induced position shift could potentially be generated in V1 or other parts of early visual cortex.

The second explanation proposes that the influence of component and global motion takes place in the same area of visual cortex, with hMT+ as a main candidate. In this framework, our results could reflect the fact that it takes a time to integrate component motion signals and resolve global motion. At the initiation of a new motion direction, and at motion reversals, perceived motion is predominantly in the local, component direction (Lorenceanu et al., 1993; Montagnini, Spering, & Masson, 2006; Pack & Born, 2001). Our dot probes were presented at motion reversals, the moment at which these brief initial component motion signals would arise. The global motion direction quickly takes over (in about 200 ms, according to Montagnini, Spering, & Masson, 2006), so component motion signals may be too short-lived to register in awareness, but they could still yield a crucial influence that makes component motion dominate the shift direction. It is not possible to test this hypothesis with the current stimulus, because the flash-grab effect depends critically on the flash occurring at the same time as the motion reversals. If another stimulus was used that was less sensitive to temporal offsets between the flash and the motion, one could test the position shift effect at various times after the motion onset, and determine if global motion will begin to dominate when given enough time. This approach was used by Roach and McGraw (2009) to answer a separate, but related, question. It might even be possible to measure the shift at different points along a moving contour, and see how the shift is affected by global motion signals propagating along the contour. Such an experiment might reveal that the position shift always follows the motion available at the point in time and space where the flash is shown. It is also possible, however, that there will always be an influence of component motion on the position shift, even when global motion is fully resolved, perhaps because motion at different stages of the visual system influence position separately, as discussed above. Future research will be necessary to resolve this important issue.

5. Conclusion

In recent years, multiple studies have explored the types of motion that can produce motion-induced position shifts. The emphasis has been on showing that position shifts are not driven exclusively by local, image-level motion signals, but can be influenced by various types of non-local signals, such as global motion. Our results are in correspondence with these findings in the sense that we also demonstrate a clear influence of global motion on the flash grab effect. When a global motion stimulus was perceived as moving horizontally or vertically, the position shift of the flash was biased in the horizontal or vertical directions, respectively. In addition, the global motion percept of vertically moving line segments led to a bigger flash grab effect than when the horizontally moving

complete diamond was seen. However, because our participants reported the magnitude and direction of the shift they perceived, we can go beyond previous work and estimate the extent to which the position shift is aligned with global motion direction. Surprisingly, we find that the motion-induced position shift is not determined by global motion alone, and that component motion in fact plays a bigger role in determining the shift direction. To our knowledge, this is the first demonstration of such a clear discrepancy between position shifts and the consciously perceived global motion.

Acknowledgment

This work was supported by a grant from the Templeton Foundation (to PUT) and grants from the ANR and ERC (to PC).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.visres.2015.03.003>.

References

- Anstis, S. M., & Mackay, D. M. (1980). The perception of apparent movement [and Discussion]. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 290(1038), 153–168.
- Born, R. T., Tsui, J. M., & Pack, C. C. (2010). Temporal dynamics of motion integration. In *Dynamics of visual motion processing* (pp. 37–54). New York: Springer.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10(4), 433–436.
- Bressler, D. W., & Whitney, D. (2006). Second-order motion shifts perceived position. *Vision Research*, 46(6–7), 1120–1128.
- Britten, K. H., Shadlen, M. N., Newsome, W. T., & Movshon, J. A. (1992). The analysis of visual motion: A comparison of neuronal and psychophysical performance. *The Journal of Neuroscience*, 12(12), 4745–4765.
- Cai, R. H., & Schlag, J. (2001a). Asynchronous feature binding and the flash-lag illusion. *Investigative Ophthalmology and Visual Science*, 42, S711.
- Cai, R. H., & Schlag, J. (2001b). A new form of illusory conjunction between color and shape. *Journal of Vision*, 1(3), 127.
- Cavanagh, P., & Anstis, S. (2013). The flash grab effect. *Journal of Vision*, 12(9), 778–778.
- Cavanagh, P., & Mather, G. (1989). Motion: The long and short of it. *Spatial Vision*, 4(2–3), 2–3.
- De Valois, R. L., & De Valois, K. K. (1991). Vernier acuity with stationary moving Gabors. *Vision Research*, 31(9), 1619–1626.
- Eagleman, D. M., & Sejnowski, T. J. (2007). Motion signals bias localization judgments: A unified explanation for the flash-lag, flash-drag, flash-jump, and Frohlich illusions. *Journal of Vision*, 7(4), 3.
- Fischer, J., Spotswood, N., & Whitney, D. (2011). The emergence of perceived position in the visual system. *Journal of Cognitive Neuroscience*, 23(1), 119–136.
- Fröhlich, F. W. (1923). Über die Messung der Empfindungszeit [Measuring the time of sensation]. *Zeitschrift für Sinnesphysiologie*, 54, 58–78.
- Hisakata, R., & Murakami, I. (2009). Illusory position shift induced by plaid motion. *Vision Research*, 49(24), 2902–2910.
- Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *The Journal of Physiology*, 160(1), 106.
- Huk, A. C., Ress, D., & Heeger, D. J. (2001). Neuronal basis of the motion aftereffect reconsidered. *Neuron*, 32(1), 161–172.
- Kohler, P. J., Caplovitz, G. P., & Tse, P. U. (2009). The whole moves less than the spin of its parts. *Attention, Perception, & Psychophysics*, 71(4), 675–679.
- Kohler, P. J., Caplovitz, G. P., & Tse, P. U. (2014). The global slowdown effect: Why does perceptual grouping reduce perceived speed? *Attention, Perception, & Psychophysics*, 1–13.
- Kourtzi, Z., & Kanwisher, N. (2000). Activation in human MT/MST by static images with implied motion. *Journal of Cognitive Neuroscience*, 12(1), 48–55.
- Lorenceau, J., & Shiffrar, M. (1992). The influence of terminators on motion integration across space. *Vision Research*, 32(2), 263–273.
- Lorenceau, J., Shiffrar, M., Wells, N., & Castet, E. (1993). Different motion sensitive units are involved in recovering the direction of moving lines. *Vision Research*, 33(9), 1207–1217.
- Mackay, D. M. (1958). Perceptual stability of a stroboscopically lit visual field containing self-luminous objects. *Nature*, 181(4607), 507–508.
- Mather, G., & Pavan, A. (2009). Motion-induced position shifts occur after motion integration. *Vision Research*, 49(23), 2741–2746.
- Maus, G. W., Fischer, J., & Whitney, D. (2013). Motion-dependent representation of space in area MT+. *Neuron*, 78(3), 554–562.
- Maus, G. W., Ward, J., Nijhawan, R., & Whitney, D. (2013). The perceived position of moving objects: Transcranial magnetic stimulation of area MT+ reduces the flash-lag effect. *Cerebral Cortex*, 23(1), 241–247.
- McDermott, J., Weiss, Y., & Adelson, E. H. (2001). Beyond junctions: Nonlocal form constraints on motion interpretation. *Perception*, 30(8), 905–923.
- McGraw, P. V., Walsh, V., & Barrett, B. T. (2004). Motion-sensitive neurones in V5/MT modulate perceived spatial position. *Current Biology*, 14(12), 1090–1093.
- Montagnini, A., Spering, M., & Masson, G. S. (2006). Predicting 2D target velocity cannot help 2D motion integration for smooth pursuit initiation. *Journal of Neurophysiology*, 96(6), 3545–3550.
- Muckli, L., Kriegeskorte, N., Lanfermann, H., Zanella, F. E., Singer, W., & Goebel, R. (2002). Apparent motion: event-related functional magnetic resonance imaging of perceptual switches and states. *Journal of Neuroscience*, 22(9), 166.
- Nakayama, K., & Silverman, G. H. (1988). The aperture problem—I. Perception of nonrigidity and motion direction in translating sinusoidal lines. *Vision Research*, 28(6), 739–746.
- Nijhawan, R. (1994). Motion extrapolation in catching. *Nature*, 370(6487), 256–257.
- Pack, C. C., & Born, R. T. (2001). Temporal dynamics of a neural solution to the aperture problem in visual area MT of macaque brain. *Nature*, 409(6823), 1040–1042.
- Pack, C. C., Gartland, A. J., & Born, R. T. (2004). Integration of contour and terminator signals in visual area MT of alert macaque. *Journal of Neuroscience*, 24(13), 3268–3280.
- Pavan, A., Cuturi, L. F., Maniglia, M., Casco, C., & Campana, G. (2011). Implied motion from static photographs influences the perceived position of stationary objects. *Vision Research*, 51(1), 187–194.
- Pavan, A., & Mather, G. (2008). Distinct position assignment mechanisms revealed by cross-order motion. *Vision Research*, 48(21), 2260–2268.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442.
- Ramachandran, V. S., & Anstis, S. M. (1990). Illusory displacement of equiluminous kinetic edges. *Perception*, 19(5), 611–616.
- Rider, A. T., McOwan, P. W., & Johnston, A. (2009). Motion-induced position shifts in global dynamic Gabor arrays. *Journal of Vision*, 9(13), 8. 1–8.
- Roach, N. W., & McGraw, P. V. (2009). Dynamics of spatial distortions reveal multiple time scales of motion adaptation. *Journal of Neurophysiology*, 102(6), 3619–3626.
- Rolls, M. (2009). Microsaccades: Small steps on a long way. *Vision Research*, 49(20), 2415–2441.
- Salzman, C. D., Britten, K. H., & Newsome, W. T. (1990). Cortical microstimulation influences perceptual judgements of motion direction. *Nature*, 346(6280), 174–177.
- Shim, W. M., & Cavanagh, P. (2004). The motion-induced position shift depends on the perceived direction of bistable quartet motion. *Vision Research*, 44(20), 2393–2401.
- Sterzer, P., Haynes, J.-D., & Rees, G. (2006). Primary visual cortex activation on the path of apparent motion is mediated by feedback from hMT+/V5. *Neuroimage*, 32(3), 1308–1316.
- Sundberg, K. A., Fallah, M., & Reynolds, J. H. (2006). A motion-dependent distortion of retinotopy in area V4. *Neuron*, 49(3), 447–457.
- Tse, P., & Hsieh, P.-J. (2006). The infinite regress illusion reveals faulty integration of local and global motion signals. *Vision Research*, 46(22), 3881–3885.
- Tse, P. U., Whitney, D., Anstis, S., & Cavanagh, P. (2011). Voluntary attention modulates motion-induced mislocalization. *Journal of Vision*, 11(3), 12.
- Watanabe, K., Nijhawan, R., & Shimojo, S. (2002). Shifts in perceived position of flashed stimuli by illusory object motion. *Vision Research*, 42(24), 2645–2650.
- Watanabe, K., Sato, T. R., & Shimojo, S. (2003). Perceived shifts of flashed stimuli by visible and invisible object motion. *Perception*, 32(5), 545–559.
- Whitney, D., & Cavanagh, P. (2000). Motion distorts visual space: Shifting the perceived position of remote stationary objects. *Nature Neuroscience*, 3(9), 954–959.
- Yin, C., Shimojo, S., Moore, C., & Engel, S. A. (2002). Dynamic shape integration in extrastriate cortex. *Current Biology*, 12(16), 1379–1385.