Attention updates the perceived position of moving objects

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Abstract

The information used by conscious perception may be somewhat different from that which drives certain actions. In support of this notion, recent studies reported that although internal grating motion can accumulate over seconds into a large illusory position shift, this position shift is not reflected in saccade targeting (action). Another possibility however is that rather than saccades and other actions having privileged access to the correct position, the attention shift thought to precede saccades resets the accumulated position shift to zero. Here we found that the accumulation of illusory position shift can be reset by transients near the moving object and also by the observer pressing a button at the time the object is perceived to reach a particular position. This creates a striking impression of the object jumping back to near its actual position. These results suggest that both stimulus-driven attention and attention associated with control of action may update the perceived position of moving objects and mediate the previously reported dissociation between conscious perception and saccades.

Results

Visual motion signals can strongly affect the perception of position. For example, texture motion within a stationary object shifts that object's position in the direction of the texture motion [1,2]. Interestingly, if such an object moves by itself in a trajectory orthogonal to the texture motion, the illusory position shift accumulates over seconds, giving a sensation of trajectory oriented between the directions of texture and object motions [3,4]. This is referred to as the curveball or double-drift illusion. Lisi & Cavanagh [5] reported that when participants are asked to move their eyes (saccade) to a double-drifting object, their eyes land in approximately the veridical position rather than the position perceived. Lisi & Cavanagh concluded that the information used by conscious perception is somewhat different from that which drives certain actions (saccades). The present study instead suggests that the attention shifts thought to precede saccades resets the accumulated position shift to zero, explaining why saccades are made to the veridical object location, and highlighting a new role for attention.

We find that both luminance and isoluminant transients near the moving object ("flash" and "color change" experiments respectively) and an observer's button press subjectively timed to the object reaching a particular position ("button-press" experiment) can reset the accumulation of illusory position shift, creating an impression of the object jumping back to its actual position. What do these manipulations have in common? Arguably, a shift of attention toward a particular location in the moving object's trajectory.

In each trial of our flash experiment, a pair of circular objects moved diagonally down on a screen and horizontally outward from a fixation point in the left and right upper visual fields respectively (Figure 1A) while internal grating patterns parallel to the object trajectories were either stationary within the circular envelopes (single-drifting objects) or drifted inward (double-drifting objects). During the single-drift trials and half of the double-drift trials, white squares were flashed on both sides of each of the two moving objects for one movie frame, which occurred at a random time between 0.7-1.1 sec after stimulus motion onset. The moving stimuli disappeared 1.8 sec after onset. Participants maintained fixation throughout (monitored by an eye tracker) and drew the object trajectories they perceived with a computer mouse. All trials containing saccades in a period from 0.7 to 1.5 sec were removed from subsequent analyses.

Figure 1B shows the trajectories reported for double-drifting objects (left column), double-drifting objects accompanied by flashes (middle column), and single-drifting objects accompanied by flashes (right column). Pink-shaded bands indicate intervals wherein flashes were presented. It can be seen that the internal grating motion of the majority of the perceived trajectories of the double-drifting objects biased the trajectories perceived toward fixation, especially in the first half of the trajectory. The appearance of the flashes (middle column) frequently results in a sharp trajectory change, sometimes described by participants as a jump, toward the true position of the object. On the other hand, single-drifting objects keep moving straight despite the flash presentation. In summary, the luminance flash frequently resets the accumulation of illusory position shift caused by double drifts.

The variance of the trajectories drawn for different trials and participants is significant. To quantitatively and reproducibly assess the proportion of trials in which a jump was indicated in the trajectory drawn, we classified them as "jump" and "no jump" trials with a likelihood-ratio test [6]: a statistical comparison of models with versus without a horizontal jump in a linear or curved course of stimulus trajectories. Specifically, a quadratic curve ($x = ay^2 + by + c$; x and y denote horizontal and vertical positions; a, b, and c are free parameters) both with and without two additional free parameters to create a horizontal jump (corresponding to the timing and the size of the jump) was fitted to each trajectory, by maximum likelihood assuming that the model's errors are normally distributed.

$$Likelihood = \prod_{i=1}^{n} \exp\left(\frac{-(x_i-\mu_i)^2}{2\sigma^2}\right) \qquad (1)$$

Here, μ and σ denote a model prediction of horizontal position (x) and standard deviation of horizontal positions, respectively. The fits of the curves were very good – on average with the jump/no-jump model r^2 = 0.970/0.962 (SE = 0.014/0.019) for double-drifting objects, 0.958/0.900 (SE = 0.012/0.030) for same objects with flashes, and 0.992/0.986 (SE = 0.002/0.004) for single-drifting objects with flashes (also see Figure S1 panels for the best-fit curves). The likelihood-ratio test was used to decide whether the jump model fit significantly better than the no-jump model. This test used the maximum likelihood for the jump and no-jump models and the following test statistic (*T)*, which follows a Chi-squared distribution (degrees of freedom = 1; the timing parameter operates fully depending on the presence/absence of the size parameter).

$$T = 2log\ (\frac{Likelihood\ with\ jump}{Likelihood\ without\ jump}) \qquad (2)$$

Perceived (sketched) trajectories were classified as "jump" paths if T values exceeded 3.84 (corresponding to $p<.05$), which are drawn in bold in Figure 1B. Figure 1C shows the proportion of the "jump" paths in each condition. Jumps were much more common for double-drifting objects with flashes compared to the other two conditions (one-way ANOVA $F_{(2,8)} = 48.92$, $p < 0.0001$; between double-drifting objects with and without flashes $t_{(8)} = 8.85$, $p < 0.0001$; between double- and single-drifting objects with flashes $t_{(8)} = 8.25$, $p < 0.0001$; between double-drifting objects without flashes and single-drifting objects with flashes $t_{(8)} = 0.60$, $p = 0.56$). For a potentially corroborating analysis, instead of using the T value to classify the trials and comparing their proportion, we compared T values between conditions directly. Circles in Figure 1C plot average T values. Similar to the classification-based analysis, the T value is significantly larger for double-drifting stimuli with flashes (one-way ANOVA $F_{(2,8)} = 16.79$, $p = 0.001$; $t_{(8)} = 4.98$, $p = 0.001$; $t_{(8)} = 5.05$, $p = 0.001$; $t_{(8)} = 0.07$, $p = 0.95$ in comparisons of the same order as above). The perceived jumps occurred around the time of the flashes (relative to the flashes' time, -0.05 ± 0.22 sec, 95% CI), based on the curve fits after scaling the vertical distance of the sketched trajectory to that of the actual trajectory.

These results indicate that presentation of the luminance flashes reset the accumulated illusory position shift, causing a jump. Why do the flashes cause a jump? It might conceivably be mediated by the first-order motion energy of the flashes [7,8], the fact that flashes can suppress certain percepts [9], or from the participant's attention being grabbed by the sudden appearance of the flashes. If it does result from stimulation of motion or luminance transient detectors, perceptual jumps may not occur without a strong luminance transient. To investigate this, in a subsequent experiment the moving objects' color was abruptly changed halfway through the trajectory after assessing equiluminance points to avoid or minimize a luminance component (Figure 2A). Such chromatic changes can attract attention [10]. As detailed below, this isoluminant chromatic change also resulted in jumps, which suggests it is a shift of attention that triggers the perceptual jump, not the luminance change.

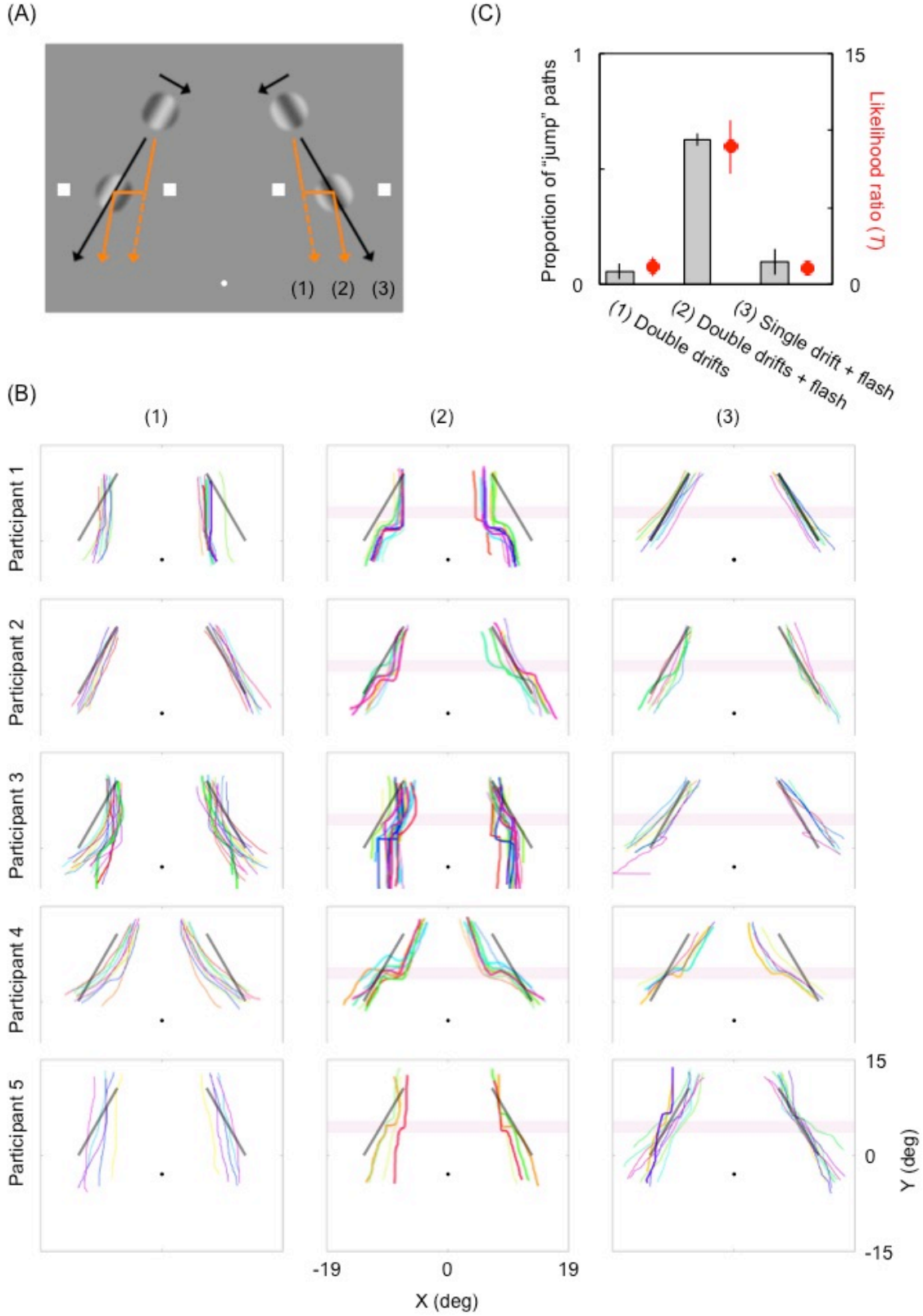

Figure 1. Schematic stimulus display and results of the flash experiment. (A) Two circular objects moved diagonally for 1.8 sec with/without orthogonal motion of internal grating patterns:

double-drifting (see Movie S1 for no flashes, Movie S2 for flashes) or single-drifting objects (see Movie S3). Black arrows indicate the physical motion directions of envelope and grating for the double-drifting objects. White squares were flashed for one screen frame between 0.7-1.1 sec after the motion began, except there was no flash in half of the double-drift trials. Orange lines (not shown during experiment) indicate possible perceived trajectories of double-drifting objects with (solid) or without (dashed) flashes, respectively. (B) Object trajectories sketched by participants. Rows correspond to participants and columns correspond to stimulus conditions. Center of screen is (0,0) in X and Y coordinates. Display colors correspond to trial numbers and bold curves denote paths classified as jumps by maximum likelihood. Black diagonal lines indicate physical trajectories and pink-shaded bands indicate spatial locations of flash presentations. (C) Bars show average proportion of perceived trajectories classified as jumps. Circles plot average likelihood ratio or *T* (right-side ordinate). Error bars represent ± 1 SE across participants.

In this chromatic change experiment, reddish and greenish objects were presented on a yellowish background adjusted to equiluminance for each participant (see Methods). During the single-drift trials and half of the double-drift trials, at a random time 0.7 to 1.1 sec into the trial, the red and green colors were swapped. Otherwise, stimulus display, drawing task, and participants were all same as the previous experiment. Trajectory data were analyzed in the same way as the previous analyses. The jump/no jump models again fit well, r^2 = 0.966/0.956 (SE = 0.021/0.023) for double-drifting objects, 0.971/0.935 (SE = 0.009/0.021) for same objects with color changes, and 0.996/0.995 (SE = 0.001/0.001) for single-drifting objects with color changes (also see Figure S2 panels for the best-fit curves).

The paths classified as jumps by the likelihood-ratio test are drawn in bold in Figure 2B. Trajectory jumps are mainly observed for double-drifting objects accompanied by color changes, except for Participant 5 who strangely shows more jumps for double-drifting objects without color changes than with them. Note that because the three types of stimulus trials are randomly interleaved, participants will have some expectation of a color change, which might result in some anticipatory attention shifts and trigger jumps in some non-color-change trials, if attention shifts cause jumps.

The proportion of trials in each condition that yielded jumps is shown by Figure 2C. Jumps occurred more often for double-drifting objects with color changes than for the other two conditions (one-way ANOVA $F_{(2,8)}$ = 7.15, p = 0.02; between double-drifting

objects with and without color changes $t_{(8)} = 2.65$, $p = 0.03$; between double- and single-drifting objects with color changes $t_{(8)} = 3.66$, $p = 0.006$; between double-drifting objects without color changes and single-drifting objects with color changes $t_{(8)} = 1.01$, $p = 0.34$). Average T values (circles) were larger for double-drifting objects with color changes than without (one-way ANOVA $F_{(2,8)} = 5.21$, $p = 0.04$; $t_{(8)} = 2.31$, $p = 0.0498$; $t_{(8)} = 3.11$, $p = 0.01$; $t_{(8)} = 0.80$, $p = 0.45$ in comparisons of the same order as above). The curve fits estimate that the jumps occurred, relative to the color changes, at 0.07 ± 0.33 sec (95% CI).

These results indicate that a sudden chromatic change in moving objects can reset the accumulation of illusory position shift caused by double drifts, despite the lack of luminance change, which reduces input to motion detectors and flash suppression processes.

The next experiment assessed whether it was truly attentional engagement with the objects, rather than something more specific to stimulus transients, that causes jumps. Participants pressed a button at the moment that moving objects arrived at a certain position. Stationary landmarks flanking that position were presented at the beginning of the trial but then removed prior to the presentation of moving objects, to eliminate the possibility of any sensory interaction. We expected that participants would particularly direct attention to the objects around the time that they should respond to them.

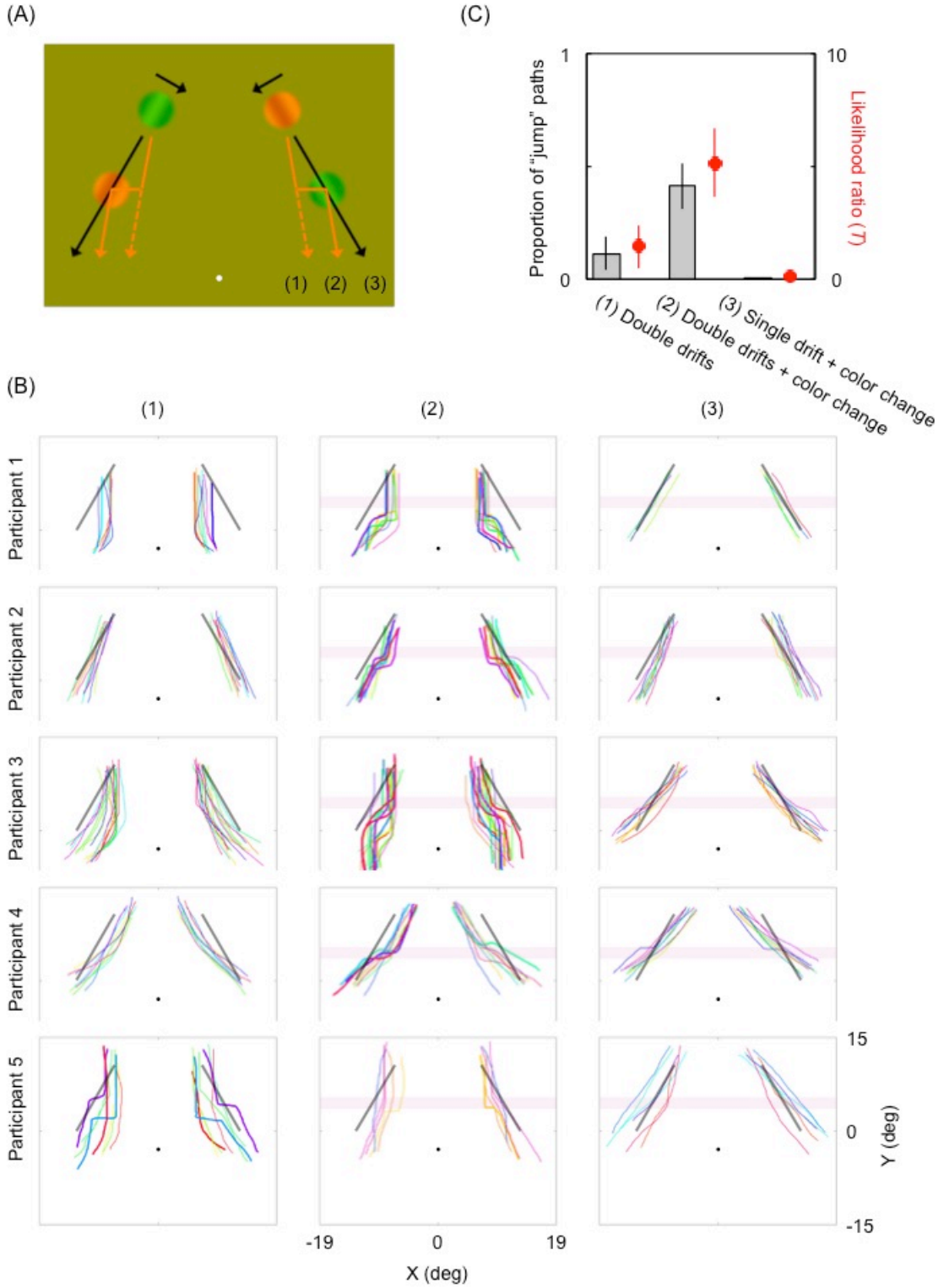

Figure 2. Schematic stimulus display and results of the color change experiment. (A) Reddish and greenish objects, with mean luminance matched to the yellowish background, moved diagonally. In the color change condition, they abruptly changed their color with each other. Other stimulus configurations were identical to those in the flash experiment. Arrows with numbers (not shown in

the experiment) indicate the predicted perceived trajectories of double-drifting objects (see Movie S4), double-drifting objects with color change (see Movie S5), and single-drifting objects with color change (see Movie S6). (B) Object trajectories sketched by participants. Black diagonal lines indicate physical trajectories and pink-shaded bands indicate region in which the color change happened. (C) Bars plot average proportion of "jump" paths (left-side ordinate). Circles plot average likelihood ratio or *T* (right-side ordinate). Error bars represent ± 1 SE across participants.

At the start of each trial, white squares were presented for 1.6 sec on both sides of the future object trajectories. After a 0.4-sec blank fixation period, the moving objects appeared. Participants were instructed to press a button with the right index finger when the moving objects passed between the former locations of the squares, while keeping their eyes on the fixation point. Other aspects were the same as the first experiment. Trajectory data were analyzed in the same way as the previous analyses, the fits for the jump/no-jump model are r^2 = 0.980/0.955 (SE = 0.005/0.011) for double-drifting objects, 0.997/0.996 (SE = 0.001/0.001) for single-drifting objects (also see Figure S3 panels for the best-fit curves).

The paths classified as jumps by the likelihood-ratio test are drawn in bold (Figure 3A). All paths classified as jumps were in the double-drifting objects condition. Bars in Figure 3B show average rates of the "jump" paths. One-way ANOVA reveals that it is significantly higher for double-drifting objects compared to single-drifting objects, $F_{(1,4)}$ = 25.02, p = 0.008. Circles in Figure 3B plot average *T* values. Similar to this classification-based analysis, one-way ANOVA indicates the *T* is larger for double-drifting objects, $F_{(1,4)}$ = 15.12, p = 0.02. The jumps occurred around the time of the button press (-0.03 ± 0.26 sec, 95% CI, relative to when the participants pressed the button), consistent with an attention shift around that time.

These results indicate that the button-press task frequently does reset the accumulation of illusory position shift caused by double drifts. This also shows that stimulus transients are not necessary for the occurrence of trajectory jumps. Putting together all the results, we suggest that a shift of attention to (close to) the moving objects resets the accumulation of illusory position shift caused by double drifts and causes a jump from the accumulated illusory position to closer to the real position.

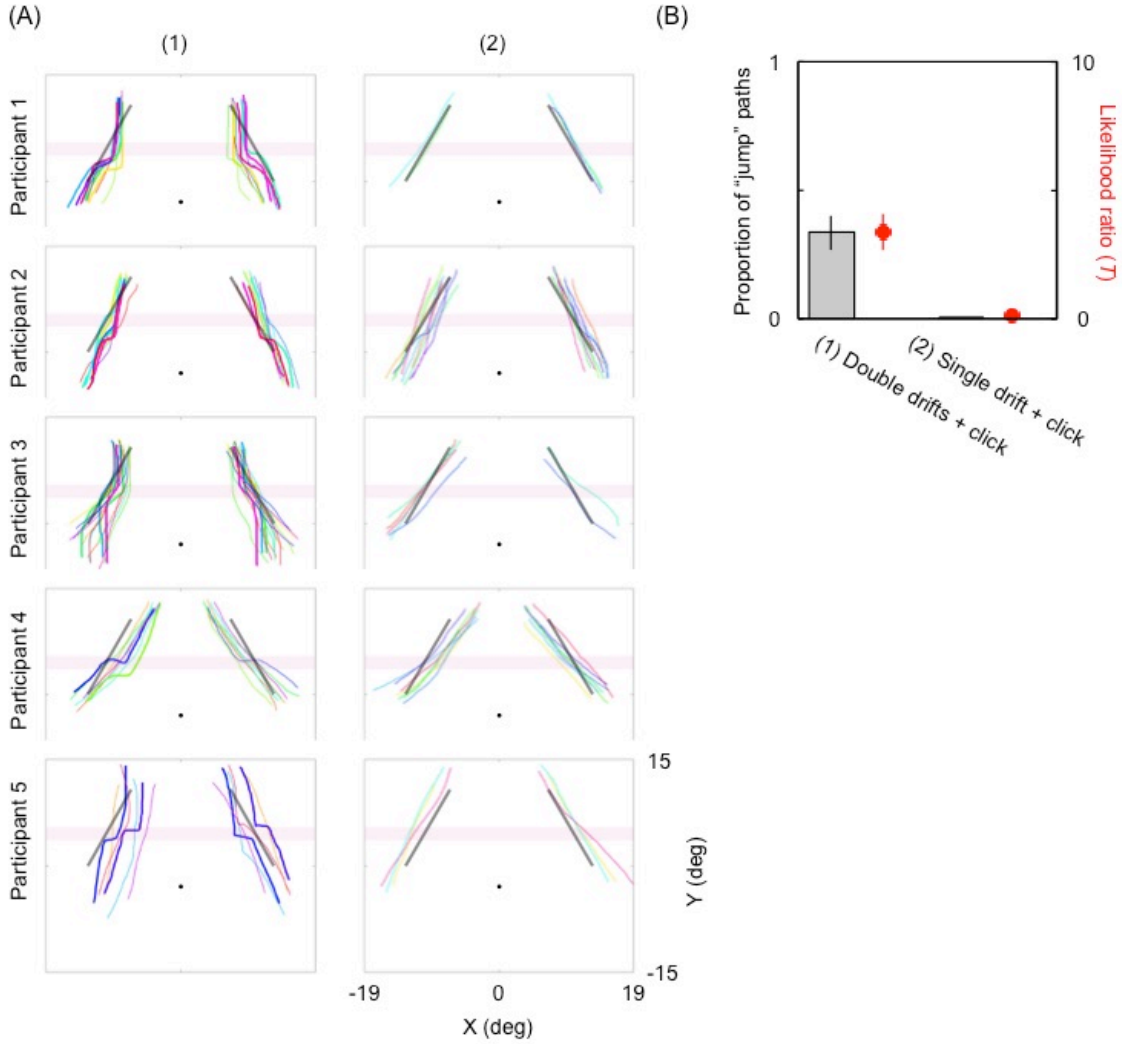

Figure 3. Results of the button-press experiment. (A) Object trajectories sketched by participants. Black diagonal lines indicate physical trajectories and pink-shaded bands indicate spatial locations of initial landmark presentations. (B) Bars plot average proportion of "jump" paths (left-side ordinate). Circles plot average likelihood ratio or *T* (right-side ordinate). Error bars represent ± 1 SE across participants.

Discussion

We have found that an accumulated illusory position shift is often reset to near zero by a luminance or chromatic transient in a moving object. This reset can also be triggered by a task involving sensorimotor reactions to a particular position of a moving object. These results are consistent with the proposition that stimulus-driven [11] and top-down attention [12] can reset the perceived position of a moving object.

Lisi & Cavanagh (2015) found that saccades to a double-drifting object were unaffected by the illusion. They suggested that this constituted the first clear and large difference between perceived position and saccade targeting, providing critical evidence for the long-running debate over how perception and action differ in their use of sensory signals. However, the present study suggests that the reason saccades are made to the correct position can be explained by the associated allocation of attention [13] rather than a dissociation between perception and action. This would also explain similar jump percepts caused by a gaze shift to a double-drifting object as described in the first report of the curveball illusion [3].

The present study hints that rather than saccades and other actions having privileged access to the correct position, perceptual and oculomotor systems rely on the same position information [14], at least in the case of this illusion. Several previous studies have investigated stationary objects with internally-drifting texture, which elicits a small position shift and relatively little accumulation [1,2,15]. One study [16], while showing that the size of the shift varies with the stimulus used to compare position to, specifically found that it is *smaller* if compared to flashed lines than if judged by actions, specifically pointing and saccades. We suggest that this result may reflect the flashed lines resetting MIPS close to zero, while the actions are guided by some information after the attention shift, during which MIPS may accumulate [15].

While an eyetracker was used to exclude trials with saccades, smaller eye movements, termed micro-saccades, may be a concern as abrupt stimulus changes induce micro-saccades [17]. However, as can be seen in Movie S7, the curveball illusion still occurs when a fixation target in motion is pursued with the eyes. Smooth pursuit regularly contains small saccades to catch up to a moving target tracked but such small jitters in retinal image seem not to reset the accumulation of position shift.

The objects in the present experiments were likely attentionally tracked by the participants throughout most trials, since the participants' task was to report their entire trajectories. Diluting attentional tracking resources among four such objects [18,19] appears to have little effect on the curveball illusion [20]. But the transients that accompany sudden visual changes have long been suggested to engage attention to a greater extent than typically occurs with top-down attention (e.g., [21]), and may even engage qualitatively different attentional functions than does top-down attention

[22,23], such as resetting the phase of ongoing oscillations [24]. However, because we found similar effects here with the button-press task that involved no transients, we suspect that a greater intensity of top-down attention causes the reset.

Why would a greater intensity of attention reset the position perceived during the curveball illusion? Attention to an object can lead to activation of the primary visual cortex neurons stimulated by that object [25], and with early cortical cells' greater spatial precision, it is adaptive to use them for position decoding. Presumably greater attention to an object activates early retinotopic cells to a greater degree. Primary visual cortex representations are shifted in the direction of object motion [26], so use of these representations should not completely eliminate the curveball illusion. However, because the amount of shift in retinotopic areas is proportional to the size of the receptive fields [26], the use of early visual cortical areas should greatly reduce the size of the illusion relative to the use of later visual cortical areas. Thus an increase in attention can cause a perceptual jump of the object towards its actual location.

Methods

Participants

Four naive participants and one of the authors (RN) participated in the experiments. All participants had normal/corrected-to-normal vision. All experiments were conducted in accordance with the Declaration of Helsinki (2003) and were approved by the ethics committee of the University of Sydney. All participants provided written informed consent.

Apparatus

Images were displayed on a gamma-corrected 22-inch CRT monitor (Mitsubishi Diamond Pro 2070SB; 1280×1024 pixel) with a frame rate of 75 Hz. The CRT pixel resolution was 1.8 min/pixel at a viewing distance of 57 cm and mean luminance was 45.8 cd/m^2. CIE chromaticity was (0.61, 0.35) in R, (0.29, 0.62) in G, and (0.15, 0.07) in B channels, respectively. Eye movements of the right eye were monitored at a sampling rate of 1000 Hz (EyeLink 1000 version 4.56; SR Research Ltd, Mississauga, Ontario, Canada).

Stimuli

Visual stimuli were a pair of sine-wave grating patterns (0.8 cycle/deg) each within a circular envelope (3.6 deg in diameter) such that grating edges would smoothly fade out into the gray background according to a quarter-cycle cosine 0.3 deg gradient. A fixation point (0.2 deg in diameter; 91.6 cd/m^2) was placed 3.0 deg below the center of screen. The envelopes (objects) moved at 6.7 deg/sec diagonally (diagonally down and outward at an angle of 30 degrees from straight down) in left and right upper visual fields respectively. Their initial position was 15.5 deg away from the fixation. The orientation of each grating was parallel to the object trajectory, its luminance contrast was 0.5, and its initial spatial phase was randomized. The grating of the double-drifting objects drifted inward at 2.2 deg/sec. For the single-drifting object, it was stationary relative to the envelope.

Procedure

All experiments were conducted in a dark room. In each trial, participants maintained gaze on the fixation point throughout the 1.8-sec presentation of the moving objects and then, after the objects disappeared, traced the object trajectories by manually dragging a computer mouse. Participants had the option to re-draw their response as many times as they liked before confirming their response. Ten trials (except for Participant 3, who participated in twenty trials) per stimulus condition were randomly interlaced in each experiment.

For the flash experiment, white squares (0.7 x 0.7 deg) were presented for 13.3 msec (one movie frame) on both sides of each of the two moving objects with horizontal offsets of 5.4 deg from them, which was randomly timed between 0.7 and 1.1 sec after the start of each trial.

For the color change experiment, instead of gray-scale grating patterns, reddish and greenish grating patterns were used against a yellowish background. The B channel was not used. The luminance contrast of the grating was 0.1 and the chromatic contrast between the reddish and greenish patterns was maximized. One of the objects was initially green, and the other initially red. The colors were initially randomly assigned to the left and right objects and then swapped at a random time between 0.7 and 1.1 sec after the start of each trial. Before the experiment started, the mean luminance of the grating was subjectively matched to the background luminance by means of flicker photometry [27] – participants minimized the subjective flicker by adjusting the green

intensity of the objects, positioned at the centers of the trajectories, alternating between the red and green colors at a rate of 8 Hz.

For the button response experiment, before the moving objects presentation, the same white squares as the flash experiment were presented for 1.6 sec then removed, followed by a blank fixation period of 0.4 sec. During the moving objects presentation, participants were told to press a button with the right-hand index finger when the objects would have passed between the squares if they had still been present. An occluder was positioned so that participants could not see their hand.

Analysis of eye movements and button presses

We removed trials that contained blinks or saccades (eye movements over 30 deg/sec or 8000 deg/sec^2) in a period from 0.7 to 1.5 sec after the start of each trial. On average, 81% (SD = 15%) of trials in the flash experiment, 87% (SD = 14%) of trials in the color change experiment, and 87% (SD = 17%) of trials in the button-press experiment were used in subsequent analyses. In the button-press experiment, a further 23% (SD = 19%) trials in which participants responded at a time that deviated from the physical alignment time by over 0.5 sec were removed.

Acknowledgments

This study was carried out when RN was a JSPS research fellow, a visiting researcher at the University of Sydney, and a visiting researcher at CiNet, NICT.

Author Contributions

RN and AOH designed the study. RN performed experiments and analyzed data. RN and AOH wrote the manuscript.

Declaration of Interests

The authors declare no competing interests.

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Supporting Information

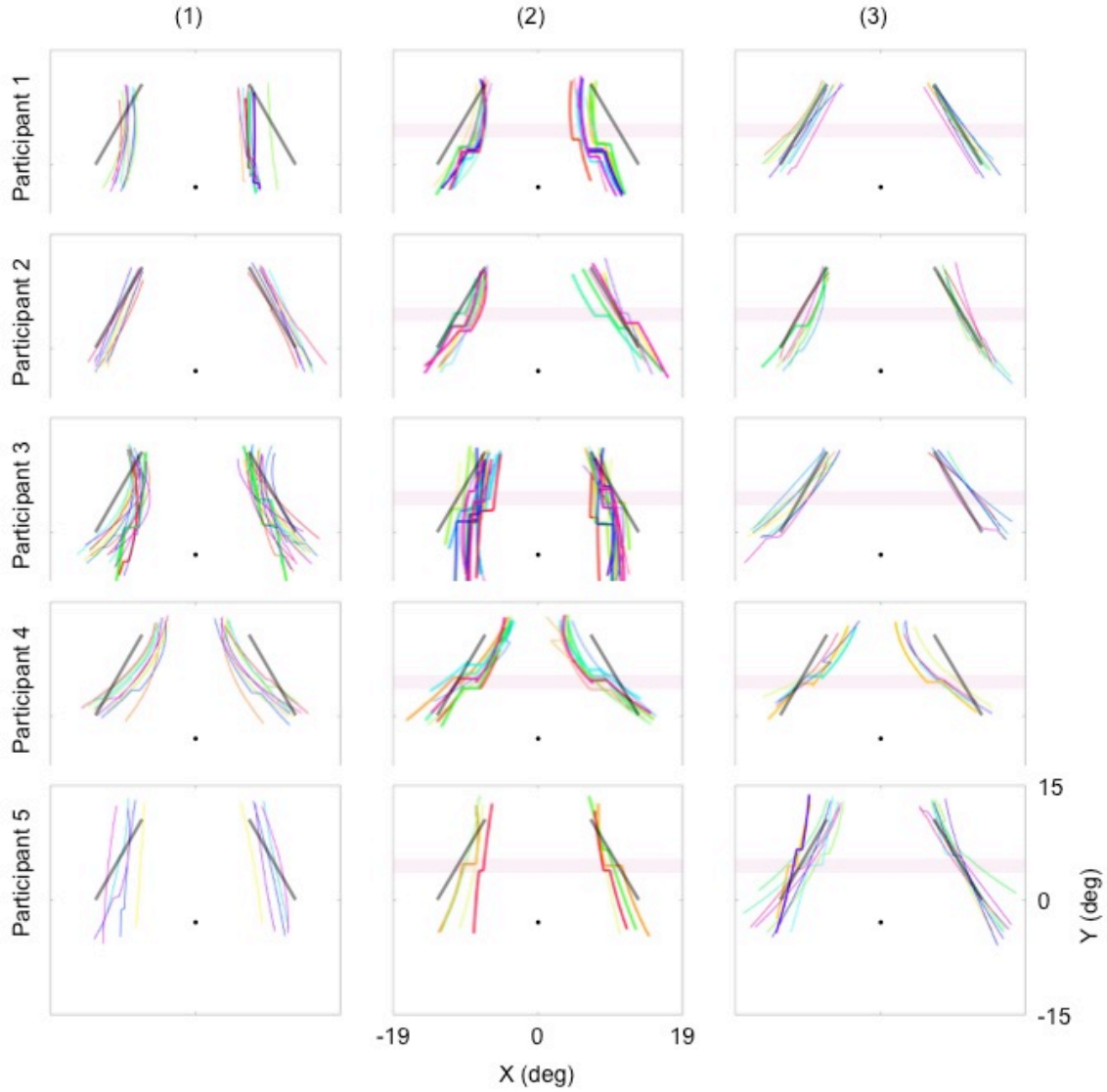

Figure S1. Best fits of object trajectories sketched by participants in the flash experiment. Rows correspond to participants and columns correspond to stimulus conditions. Center of screen is (0,0) in X and Y coordinates. Display colors correspond to trial numbers and bold curves denote paths classified as jumps by maximum likelihood. Black diagonal lines indicate physical trajectories and pink-shaded bands indicate spatial locations of flash presentations.

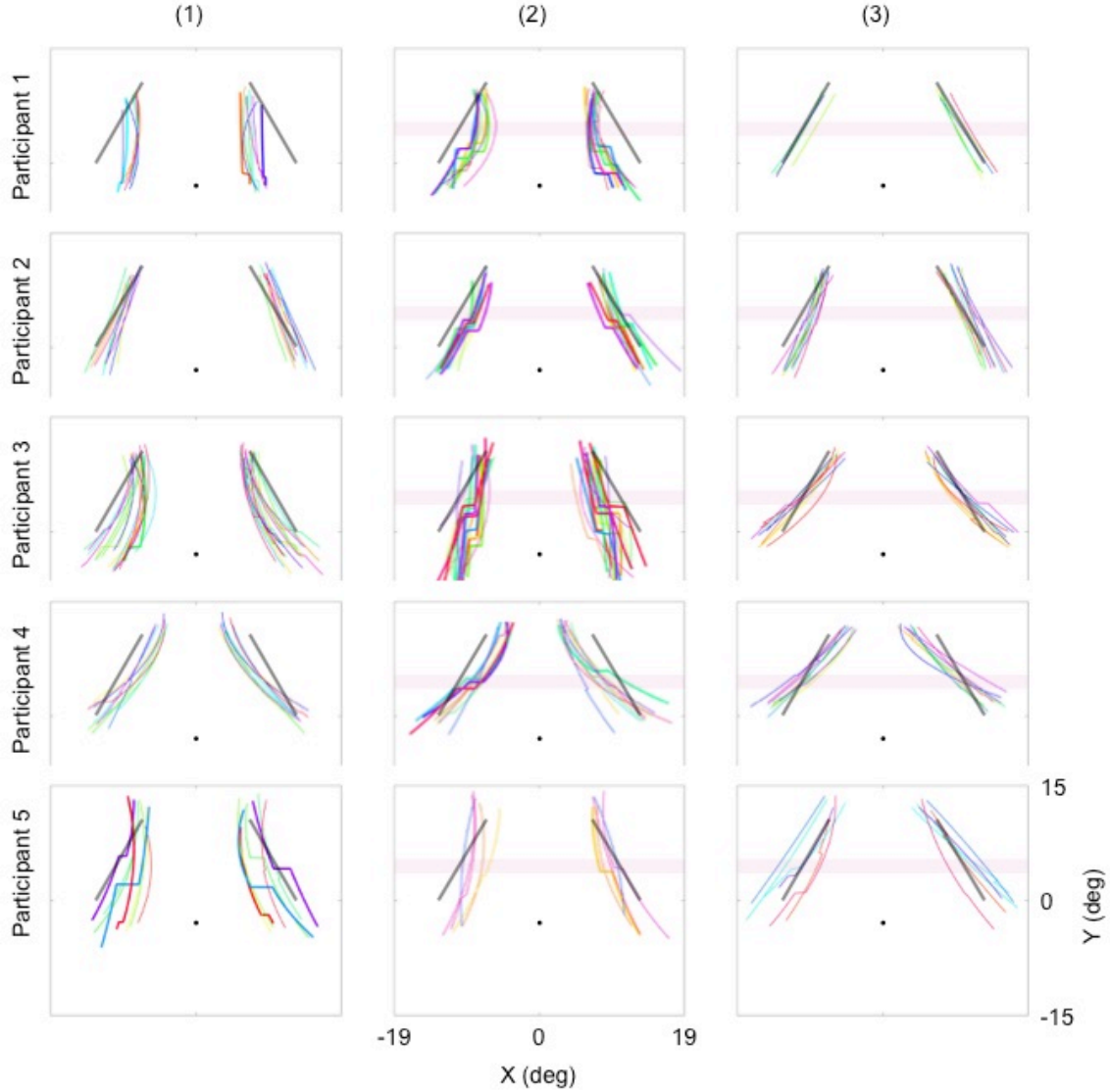

Figure S2. Best fits of object trajectories sketched by participants in the color change experiment. Rows correspond to participants and columns correspond to stimulus conditions. Center of screen is (0,0) in X and Y coordinates. Display colors correspond to trial numbers and bold curves denote paths classified as jumps by maximum likelihood. Black diagonal lines indicate physical trajectories and pink-shaded bands indicate region in which the color change happened.

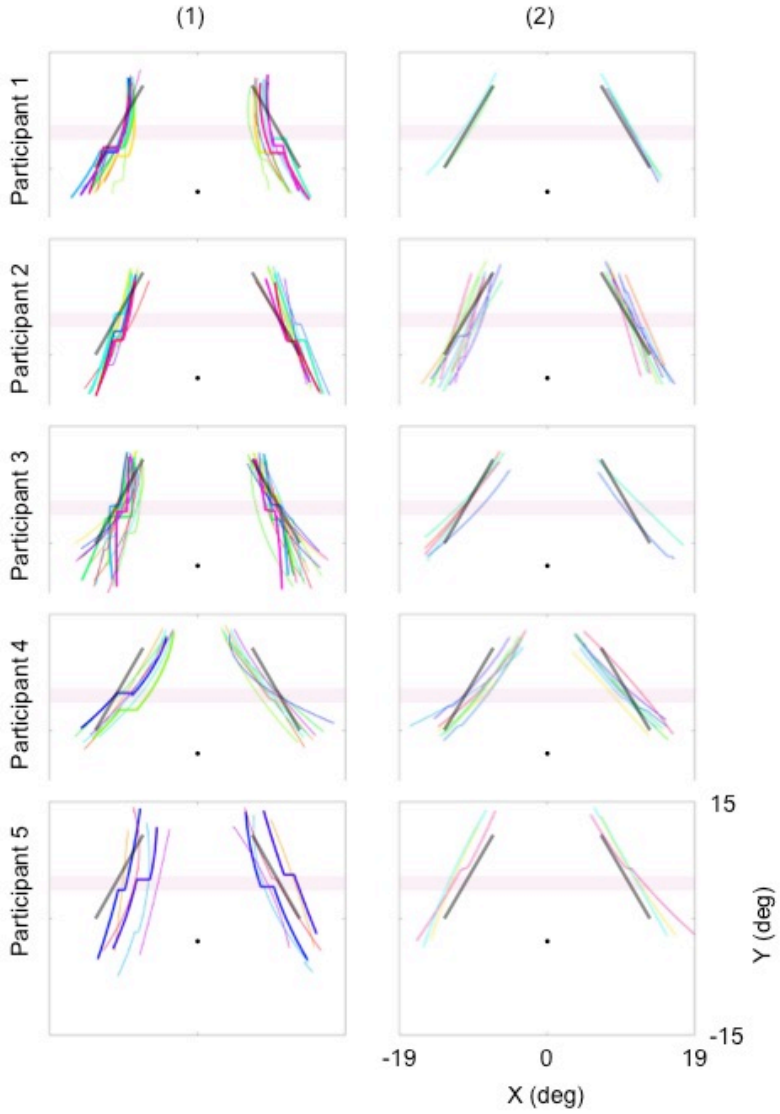

Figure S3. Best fits of object trajectories sketched by participants in the button-press experiment. Rows correspond to participants and columns correspond to stimulus conditions. Center of screen is (0,0) in X and Y coordinates. Display colors correspond to trial numbers and bold curves denote paths classified as jumps by maximum likelihood. Black diagonal lines indicate physical trajectories and pink-shaded bands indicate spatial locations of initial landmark presentations.

Movie S1. Double-drifting objects. Texture motion accumulates over seconds into a large illusory position shift of objects, whose diagonal trajectories are perceived as straight down or slightly slanted in periphery (curveball illusion).

Movie S2. Double-drifting objects accompanied by flashes. Accumulated position shift is reset to near zero by luminance flashes, causing jump percepts in object trajectories.

Movie S3. Single-drifting objects accompanied by flashes. Diagonal trajectories are perceived mostly as they are regardless of luminance flashes (control condition).

Movie S4. Chromatic double-drifting objects. Texture motion accumulates over seconds into a large illusory position shift of objects, whose diagonal trajectories are perceived as straight down or somewhat slanted in periphery (curveball illusion).

Movie S5. Chromatic double-drifting objects accompanied by color changes. Accumulated position shift is reset to near zero by color changes (adjusted to equiluminance in the experiment), causing jump percepts in object trajectories.

Movie S6. Chromatic single-drifting objects accompanied by color changes. Diagonal trajectories are perceived mostly as they are regardless of color changes (control condition).

Movie S7. Double-drifting objects with a smooth-pursuing target. Curveball illusion occurs during smooth pursuing with the eyes a target in horizontal motion.