Ocular torsion is related to perceived motion-induced position shifts

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Abstract

Ocular torsion, rotations of the eye about the line of sight, can be induced by visual rotational motion. It remains unclear whether and how such visually-induced torsion is related to perception. By utilizing the flash-grab effect, an illusory position shift of a briefly flashed stationary target superimposed on a rotating pattern, we examined the relationship between torsion and perception. In two experiments, 25 observers reported the perceived location of a flash while their three-dimensional eye movements were recorded. In experiment 1, the flash coincided with a direction reversal of a large, centrally-displayed, rotating grating. The grating triggered visually-induced torsion in the direction of stimulus rotation. The magnitude of torsional eye rotation correlated with the illusory perceptual position shift. To test whether torsion caused the illusion, in experiment 2, the flash was superimposed on two peripheral gratings rotating in opposite directions. Even though torsion was eliminated, the illusory position shift persisted. Despite the lack of a causal relationship, the torsion-perception correlations indicate a close link between both systems, either through similar visual-input processing or a boost of visual rotational signal strength via oculomotor feedback.

Ocular torsion is related to perceived motion-induced position shifts

Torsional eye movements are rotations of the eye about the line of sight that accompany almost every gaze shift (Ferman, Collewijn, & Van den Berg, 1987; Haustein, 1989; Lee, Zee, & Straumann, 2000; Straumann, Zee, Solomon, & Kramer, 1996; Tweed, Fetter, Andreadaki, Koenig, & Dichgans, 1992; Tweed & Vilis, 1990). Torsion can also be driven by rotations of the head or whole body (Bockisch, Straumann, & Haslwanter, 2003; Crawford, Martinez-Trujillo, & Klier, 2003; Misslisch & Hess, 2000; Misslisch, Tweed, Fetter, Sievering, & Koenig, 1994) or by exposure to radial motion (Edinger, Pai, & Spering, 2017; Farooq, Proudlock, & Gottlob, 2004; Ibbotson, Price, Das, Hietanen, & Mustari, 2005; Sheliga, Fitzgibbon, & Miles, 2009). In humans, torsional eye movements are typically small and slow, with velocity gains commonly reported to be below 0.1, and are therefore usually disregarded in visual psychophysics and eye movement experiments.

However, some studies have shown that torsional eye position influences visual perception. For example, when asked to judge the orientation of a tilted line, observers' judgments were biased in the opposite direction of torsion, indicating that torsional eye position was taken into account during this task (Haustein & Mittelstaedt, 1990; Murdison, Blohm, & Bremmer, 2017; Nakayama & Balliet, 1977; Wade & Curthoys, 1997). In these studies, torsion was induced by moving the eyes to a tertiary (oblique) location (Haustein & Mittelstaedt, 1990; Murdison et al., 2017; Nakayama & Balliet, 1977) or by whole-body rotations (Wade & Curthoys, 1997). Oblique eye position-induced torsion is the by-product of eye rotations as described by Listing's law (Ferman et al., 1987; Haustein, 1989), and self-motion induced torsion is modulated by the vestibular system (Leigh & Zee, 2015). By contrast, visually-induced torsion—eye rotations that are triggered by viewing rotating visual objects—may involve different mechanisms and cortical pathways. The relationship between this type of torsion and visual perception has not yet been studied. The goal of the present study is to investigate whether and how visually-induced torsion relates to visual motion perception.

Indirect evidence for the proposed torsion-perception link comes from two sets of studies. The first shows a tight link between smooth pursuit eye movements—the eyes' key response to visual motion—and motion perception (Kowler, 2011; Schütz, Braun, & Gegenfurtner, 2011; Spering & Montagnini, 2011). For example, pursuit and perception respond similarly to visual illusions such as the motion aftereffect (Braun, Pracejus, & Gegenfurtner, 2006; Watamaniuk & Heinen, 2007). Pursuit and perception are assumed to share early-stage motion processing in middle temporal visual area (MT) and medial superior temporal area (MST; Ilg, 2008; Lisberger, 2015). The second study shows a tight link between pursuit and visually-induced torsion: Edinger et al. (2017) demonstrated that smooth pursuit velocity gain depended on the magnitude of visually-induced torsion during pursuit, and that torsional and horizontal corrective saccades were synchronized. These findings were obtained with a paradigm that induced pursuit and torsion via rapid rotation of a visual stimulus that also translated across the screen (akin to a rolling ball). It is noteworthy that ocular torsion induced by eye position/head roll can be compensated during pursuit (Blohm & Lefèvre, 2010).

Because of the close link between pursuit and perception, and between pursuit and visually-induced torsion, we hypothesize that visually-induced torsion might also be linked to visual motion perception. To examine this connection, we took advantage of an illusion induced by visual rotational motion: the flash-grab effect (Blom, Liang, & Hogendoorn, 2019; Cavanagh & Anstis, 2013; Hogendoorn, Verstraten, & Cavanagh, 2015; van Heusden, Rolfs, Cavanagh, & Hogendoorn, 2018). This illusion relies on the presentation of a rotating grating, which changes rotational direction at some point during presentation. When a second object is flashed briefly on the grating at the time of direction reversal, the perceived location of the flashed object will be shifted in the direction of the grating's rotation after reversal. This perceptual illusion has been shown to be linked to properties of saccadic eye movements. For example, van Heusden et al. (2018) asked observers to perceptually report the location of the flash or to make an eye movement towards it. Their results showed that the perceived flash locations matched saccade endpoints and that the magnitude of the perceived position shift was correlated with saccade latencies.

Whereas saccades have frequently been linked to perceptual phenomena such as motion-induced illusions (e.g., Becker, Ansorge, & Turatto, 2009; de'Sperati & Baud-Bovy, 2008; Zimmermann, Morrone, & Burr, 2012), ocular torsion has not been directly assessed in studies investigating perceptual illusions. Here we measured torsional eye movements during the flash-grab effect. In two experiments, we tested whether and how the magnitude of the perceptual illusion was correlated with the strength of the torsional response. In experiment 1, the flash grab-effect was elicited by a large centrally-displayed rotating grating, which is expected to trigger ocular torsion. A correlation between perceived position shifts in the direction of the illusion and the strength of the torsional response would suggest similar processing of rotational motion information for perception and torsion. In experiment 2, we investigated whether a causal relationship exists between torsion and perception. We displayed two gratings that rotated in opposite directions. This setup is likely to elicit the perceptual illusion, as shown previously for the flash-drag effect (Whitney & Cavanagh, 2000). These authors simultaneously presented two pairs of linear gratings moving in opposite directions, each with a flash superimposed, and found that the illusion persisted even though it was weaker. They suggested that eye movements were unlikely the cause of the illusion, since the eyes could not follow opposite directions. However, torsional eye movements were not measured. It remains possible that cyclovergence, torsional eye movements in opposite directions, could have been induced (Somani, DeSouza, Tweed, & Vilis, 1998; Banks, Hooge, & Backus, 2001). Therefore, in experiment 2, torsion in the presence of a persisting illusion would confirm the link with perception. By contrast, a lack of torsion in the presence of a persisting illusion would indicate that torsion does not cause the perceptual illusion.

Methods

Observers

We tested 15 observers (mean age 25.4 ± 7.5 years, three males) in experiment 1, and ten observers (mean age 24.3 ± 5.5 years, two males) in experiment 2; all had normal visual acuity as per self-report. Observers had no history of ophthalmic, neurologic, or psychiatric disease. Experimental procedures followed the tenets of the Declaration of Helsinki and were approved by the University of British Columbia Behavioral Research Ethics Board. All observers participated after giving written informed consent and received $15 CAD as compensation.

Set-up

Observers viewed stimuli in a dimly-lit room on a gamma-corrected 19-inch CRT monitor set to a refresh rate of 85 Hz (ViewSonic Graphic Series G90*f*B, 1280×1024 pixels, 36.3 × 27.2 cm; ViewSonic, Brea, CA, USA). The viewing distance was 37 cm in experiment 1. Viewing distance in experiment 2 was increased to 45 cm following initial reports that two oppositely rotating stimuli at close proximity caused dizziness. All stimuli were shown on a uniform dark grey background (17 cd/m^2). Each observer's head was stabilized using a chin rest. Stimuli and procedure were programmed in MATLAB Version R2015b (The MathWorks, Inc., Natick, MA, USA) and Psychtoolbox Version 3 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

Visual stimuli and procedure

Figure 1 shows the timeline of one experimental trial for each experiment. The flash-grab effect was triggered by presenting one rotating grating in the center of the screen in experiment 1 (**Fig. 1a**), or two gratings, each centered at an offset of 10.5° relative to the center of the screen in experiment 2 (**Fig. 1b**). Each grating was an eight-cycle square-wave grating with Michelson contrast 0.25 (average luminance 50 cd/m^2). The grating in experiment 1 was 23.6° in diameter and rotated at one of five speeds (25, 50, 100, 200, 400°/s). The two gratings in experiment 2 each had a diameter of 20°, rotating simultaneously at the same speed (25, 50, 100, or 200°/s) but in opposite directions. In both experiments, each stimulus' rotational direction reversed from clockwise (CW) to counterclockwise (CCW) or vice versa. At the reversal of rotational direction, a flash stimulus (two red disks, each with diameter of 2.5°, one shown at 12 o'clock, the other at 6 o'clock) was briefly superimposed on each grating for nine frames (~45 ms). The grating remained stationary while the flash was presented.

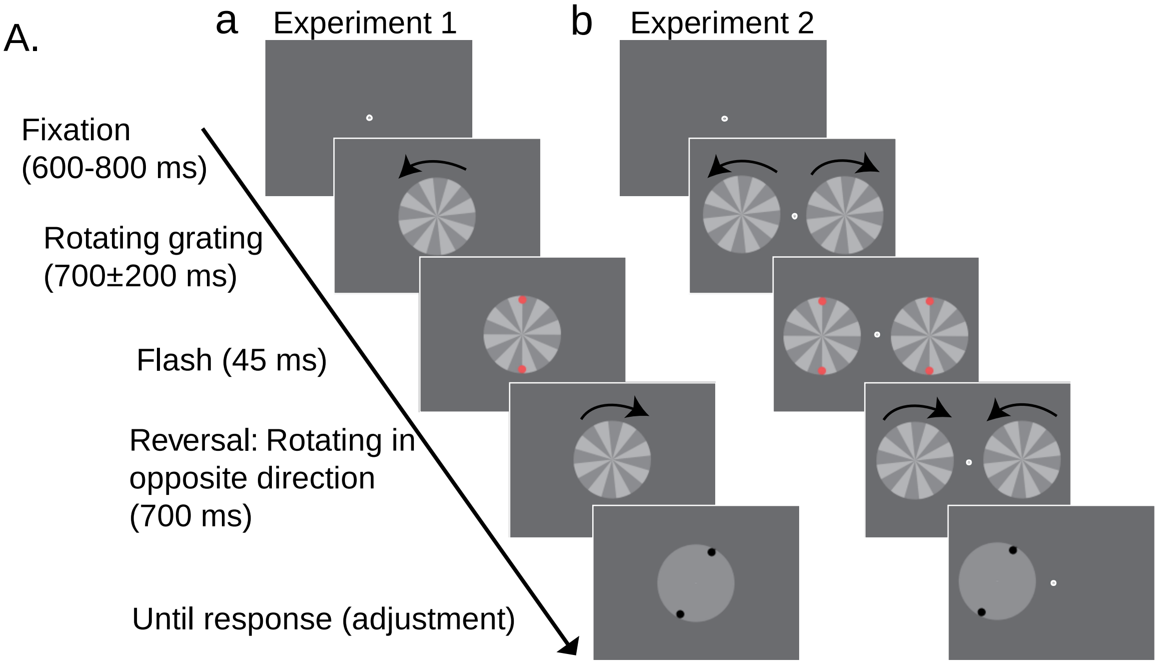

Figure 1. Trial timeline in **(a)** experiment 1 and **(b)** experiment 2. Rotating grating(s) were presented after a 600-800 ms fixation interval. Following a period of continuous motion in one direction for 500-900 ms, the flash was presented just before the grating's direction reversed. Each trial ended with the observer's response following the reference stimulus prompt. In experiment 2, observers only reported perception on the side of the reference stimulus.

At the end of each trial, observers were instructed to align a reference stimulus (two black disks, same size as flash disks) with the perceived location of the flash as accurately as possible by rotating it using a trackball mouse. The starting position of the reference stimulus was varied randomly within 45° from vertical in either direction (CW or CCW) to avoid directional judgment bias. In experiment 2, the reference stimulus was presented randomly at one of the two grating locations (left or right from the screen center), and observers were asked to estimate the perceived location of the flash on that side.

In both experiments, observers were asked to maintain fixation in the screen center and to not blink during the stimulus display. The fixation target was a white bull's eye (80 cd/m^2), with an inner circle diameter of 0.3° and an outer annulus diameter of 1°. Five experimental blocks (60 trials per block, 12 repetitions per speed) were presented in experiment 1, and six experimental blocks (48 trials per block, 12 repetitions per speed) were presented in experiment 2. Visual rotational speed and after-reversal rotational directions were counterbalanced within each block of trials.

Baseline tasks for perception and eye movements

To account for possible response bias during the perceptual reports, we conducted a baseline-perception block (60 trials) before experimental blocks. This block also served as a practice block for perceptual reports with the trackball mouse. In baseline-perception trials, observers reported the perceived location of a flash following the presentation of a stationary uniform grey disk (luminance 50 cd/m^2); the timeline was identical to experimental trials. The flash was tilted away from vertical in either direction (CW or CCW) and presented at one of five angles (2, 4, 8, 12, 16°) in experiment 1. In experiment 2, the flash was shown at one of three angles (2, 8, or 16°) but tilted in opposite directions on the left and right disk. Orientation of the flash was counterbalanced. Only perceptual judgments were analyzed in these trials and served as response bias baseline for each observer's perceptual judgments in experimental trials.

We also included a baseline-torsion block, in which observers were asked to fixate in the screen center and passively view a grating that rotated continuously for 1800-2200 ms. The gratings had the same properties as described for experiments 1 and 2. The purpose of baseline-torsion was to confirm that the rotating gratings successfully elicited visually-induced torsional eye rotations. After each trial, a reference stimulus was still presented, but no perceptual task was required. Only torsional eye movements were analyzed in these baseline trials.

Perceptual data bias correction

For analysis and illustration purposes, trials across different rotational directions were collapsed so that the after-reversal rotational direction in experimental trials was always CW. The illusory position shift in experimental trials was calculated as the bias-corrected reported angle in the after-reversal rotational direction. The response bias was corrected individually by subtracting the bias obtained in the baseline-perception block. In the baseline block, we presented flash stimuli tilted by a maximum of 16°, corresponding to the average size of the perceptual illusion (Cavanagh & Anstis, 2013). The physical tilt angle of the flash is denoted as $A_{physical}$, and the reported angle is denoted as $A_{perceived}$. A linear function $A_{perceived} = aA_{physical} + b$ was fitted to individual data. In experimental trials, we used the following function to estimate $A_{physical}$ using $A_{perceived}$, based on each observer's fitted parameters a and b:

$$A_{physical} = \begin{cases} \dfrac{A_{perceived} - b}{a}, A_{perceived} < 16a + b \\ \dfrac{16 - b}{a}, A_{perceived} \geq 16a + b \end{cases} .$$

Here we simply assumed that the response bias of a perceived angle larger than 16° remains the same as the bias of 16°. Since the illusory position shift was mostly under

25° in the current experiment, such an assumption might result in a conservative estimate of the response bias by underestimating the bias for angles larger than 16°.

Eye movement recording and analysis

Binocular eye movements were recorded with a Chronos eye-tracking device (Chronos Vision, Berlin, Germany) at a sampling rate of 200 Hz. The Chronos eye tracker is a noninvasive, head-mounted device that can record eye position including torsional eye rotations through a video-based high-resolution system (tracking resolution <0.05° along all three axes). All eye position data in experiment 1 were obtained from observers' right eyes. We previously confirmed that there are no systematic differences in visually-induced torsion between both eyes when a single rotating stimulus is presented (Edinger et al., 2017). In experiment 2, data from both eyes were analyzed. However, in order to examine the relationship between perceptual reports and torsion in a comparable way to experiment 1, we analyzed data from the eye that corresponded to the side of the target in each trial. For example, if following rotation of the two gratings the response was indicated on the right (target), we analyzed data from the right eye for this trial. If there were any differences between the eyes due to different distances to the two stimuli etc., movements of the eye on the same side as the target were likely to reflect the response of the ocular system to the target better. Across experiments and trials, intorsion of the left eye and extorsion of the right eye, corresponding to a CW visual rotation, were defined as positive by convention.

The 3D eye position data were processed offline using the Chronos Iris software (version 1.5). Torsional eye position data were derived from interframe changes in the iris crypt landmark: six segments (three on each side of the pupil) were fitted to the image of the iris, and angular eye position was calculated as a weighted average from all segments with a cross-correlation factor of >0.7 in that frame (Edinger et al., 2017). Using custom-made functions in MATLAB, torsional eye position and velocity data were filtered with a second-order Butterworth filter (cutoff 15 Hz for position, 30 Hz for velocity). Visually-induced torsion in response to rotational motion usually consists of smooth tracking movements in the target's rotational direction interspersed with saccades or quick phases in the opposite direction to reset the eye (Edinger et al., 2017). Torsional saccades were defined as a minimum of three consecutive frames exceeding an eye velocity of 8°/s. The onset and offset of torsional saccades were defined as the nearest reversal in the sign of acceleration on either side of the interval. Torsional velocity was calculated as the mean velocity during saccade-free intervals. Trials with blinks, fixation errors (eye position shift larger than 2°), loss of signals, or torsion detection error (unable to track iris segments due to pupil dilation, eye lid/lashes coverage, etc.) during the stimulus rotation were manually labeled as invalid and excluded (27.5% across experiments, eyes, and observers).

Eye movements in experimental trials were analyzed in two time windows separated by the reversal of visual rotation (see **Fig. 2**): before reversal (initial torsion onset to flash onset) and after reversal (after-reversal torsion onset to rotation offset). Torsional velocity was calculated separately for each analysis interval shown in **Figure 2**. Because the magnitude of torsional rotations was small, torsion latency was defined based on each individual observer's mean torsional velocity trace for each rotational speed. For each analysis interval, the first point when mean torsional velocity exceeded

0.1°/s was defined as torsion onset. This analysis was conducted in a time interval from 80 ms after motion onset to motion offset, because the human torsional ocular following response, a fast reflexive response to large-field rotational motion, has a latency of ~80 ms (Sheliga et al., 2009). In experiment 2, torsional eye movements were not expected to follow a consistent motion direction. Therefore, we defined torsion onset as the mean torsion latency for each rotational speed from experiment 1.

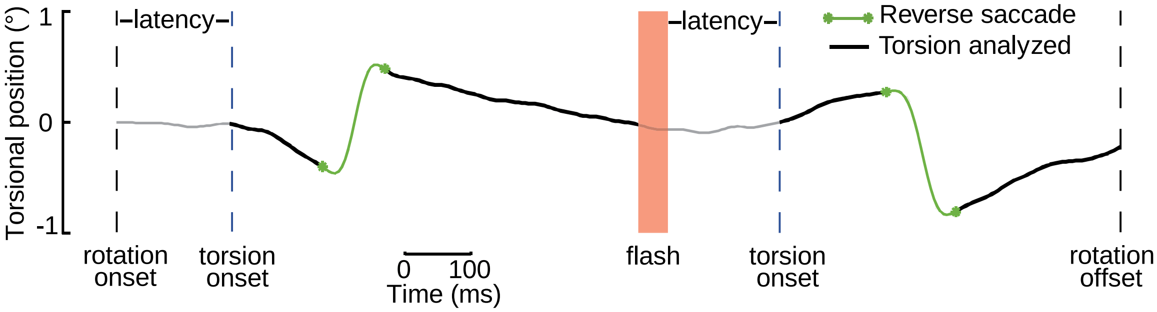

Figure 2. Example of torsional eye position in one experimental trial from experiment 1. The visual rotation was initially CCW, then CW. Flash onset corresponds to the offset of before-reversal motion, and flash offset corresponds to the onset of after-reversal motion. Bolded black segments of the line indicate the saccade-free torsion phase that is included in the analysis of torsional velocity.

Hypotheses and statistical analysis

In both experiments, we tested how perception and torsion responded to rotational motion, and analyzed the relationship between the magnitude of the illusory position shift and torsional velocity. If perception and torsion share motion processing inputs, they should be similarly affected by visual rotational speeds, i.e., increases in the magnitude of the perceptual illusion with increasing rotational speed should be accompanied by increases in torsional velocity. Correspondingly, the strength of the perceptual illusion should be correlated with torsional velocity. To investigate these hypotheses, we used within-subjects repeated-measures analysis of variance (ANOVA) to examine effects of visual rotational *speed* on illusory position shift and torsional velocity. Effect sizes were reported as generalized eta-squared (η_g^2) for all ANOVAs (Bakeman, 2005). Pearson’s correlations were calculated to assess the relationship between illusory position shift and torsional velocity across observers. Partial correlations were calculated with speed as a co-variate. Statistical analyses were conducted in R Version 3.5.1 (R Core Team, 2013; package 'ez', Lawrence, 2016; package 'ppcor', Kim, 2015).

Results

Experiment 1

A single rotating grating induced the flash-grab effect and ocular torsion

The rotating stimulus in experiment 1 successfully triggered the flash-grab effect: observers perceived the flash to be tilted in the after-reversal motion direction, as indicated by all data points lying above zero shown in **Figure 3**. The magnitude of the illusory position shift increased with increasing rotational speed, confirmed by a main effect of *speed* ($F(4, 56) = 53.26$, $p = 1.90*10^{-18}$, $\eta_g^2 = 0.55$). These results replicate previous reports of the flash-grab effect (Cavanagh & Anstis, 2013).

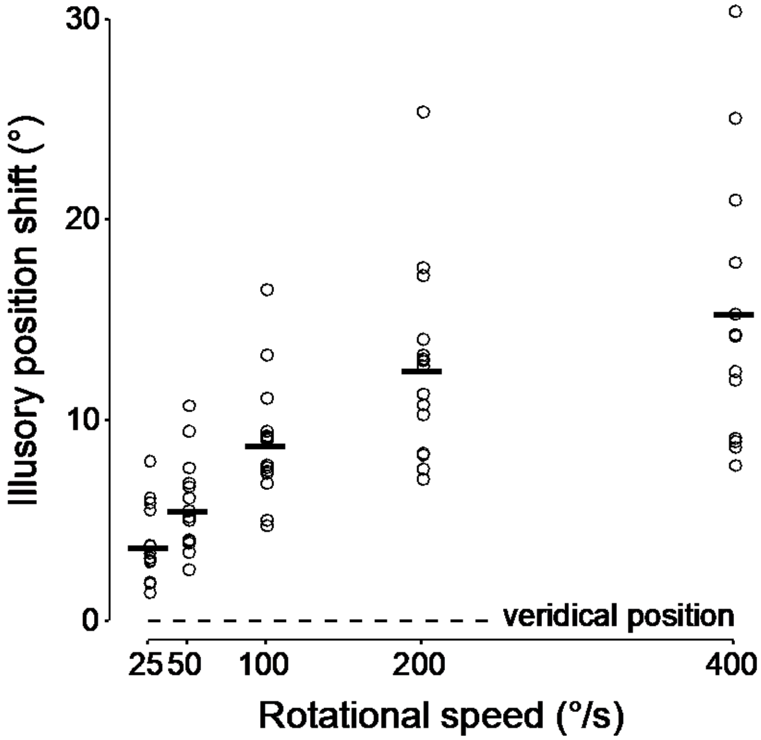

Figure 3. Illusory position shift across rotational speeds in experiment 1 (*n* = 15). Horizontal lines indicate mean illusory position shift across observers, i.e., the perceived angle of the flash stimulus. The circles indicate the mean illusory position shift of individual observers. The dashed line indicates the veridical physical angle of the flash.

The single rotating grating induced reliable ocular torsion in the direction of visual stimulus rotation. **Figure 4a** shows mean velocity traces averaged across all observers separately for the five rotational speeds. Congruent with the observed effect of rotational stimulus speed on the strength of the perceptual illusion, rotational speed also affected how fast the eye rotated. Torsional velocity increased with increasing speed, saturating at a rotational speed of 200°/s (**Figure 4b**). This observation is reflected in a significant main effect of *speed* before and after the reversal for torsional velocity (before reversal: $F(4,56) = 7.83$, $p = 4.33 * 10^{-5}$, $\eta_g^2 = 0.04$; after reversal: $F(4,56) = 9.10$, $p = 9.77 * 10^{-6}$, $\eta_g^2 = 0.06$).

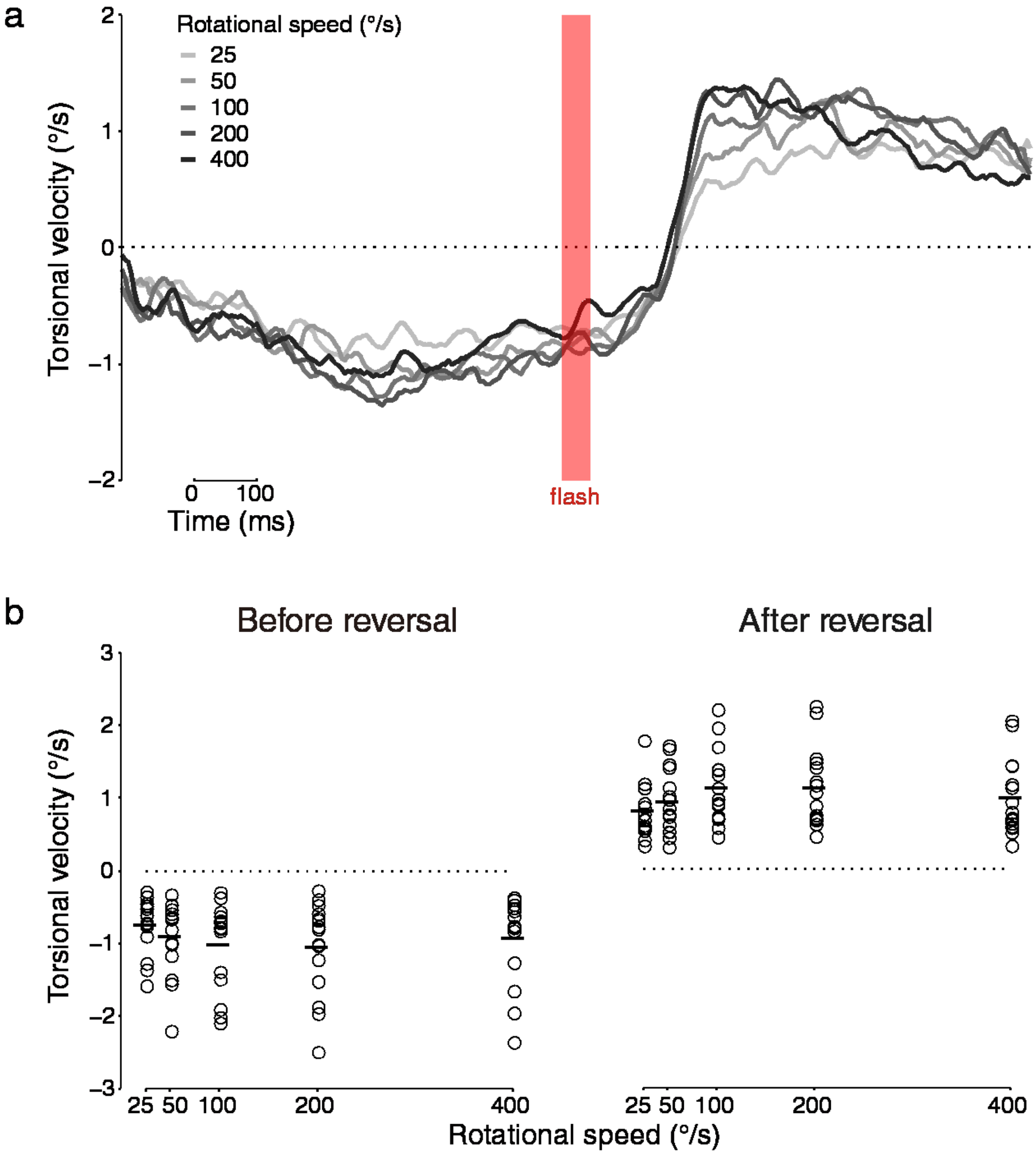

Figure 4. (a) Torsional velocity traces averaged across all observers (*n* = 15) in experiment 1. Each color indicates one rotational speed. Peak of torsional velocity scaled with rotational speeds. (b) Mean torsional velocity for each observer; same figure format as Figure 3.

To examine the correlation between perception and torsion, we calculated Pearson's correlation coefficients across observers between torsional velocity and illusory position shift, with *speed* as a co-variate. Significant correlations were found for both time windows (before reversal: r = -.49, p = 7.57*10^{-6}; after reversal: r = .59, p = 4.29*10^{-8}; see **Figure 5**). Generally, observers with faster torsional eye rotations also perceived larger illusory position shifts. To confirm that the correlation was not caused by *speed*, we also calculated Pearson's correlation coefficients using the collapsed data across speeds of each participant (one data point for each participant); significant correlations were still found for both time windows (before reversal: r = -.56, p = .03; after reversal: r = .63, p = .01). In summary, results from experiment 1 show that torsional velocity and perceptual illusion are correlated. We next investigated whether a causal relationship exists between them.

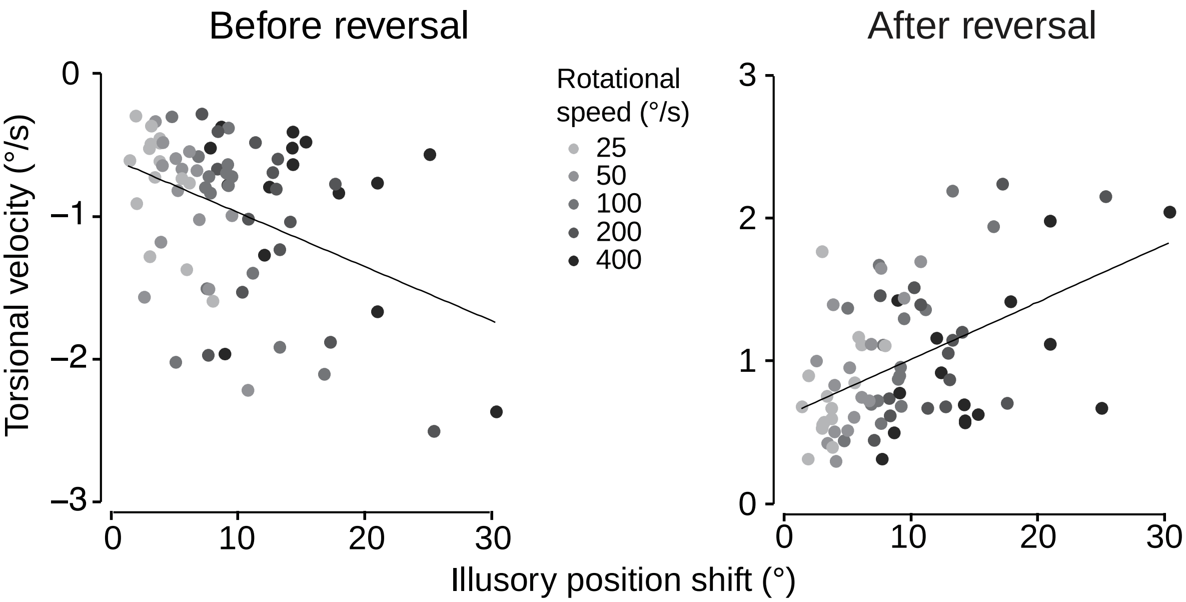

Figure 5. Correlation between torsional velocity and illusory position shift in experiment 1 in both time windows. Each data point indicates the mean data of one speed of one observer. Black lines indicate best linear fit.

Experiment 2

<u>Two rotating gratings induced the flash-grab effect in the absence of ocular torsion</u>

The gratings shown in experiment 2 produced a similar illusory position shift as in experiment 1 (see **Figure 6**). The magnitude of the illusory position shift increased with increasing rotational speed, confirmed by a main effect of *speed* ($F(3, 27) = 58.10$, $p = 6.63*10^{-12}$, $\eta_g^2 = 0.26$).

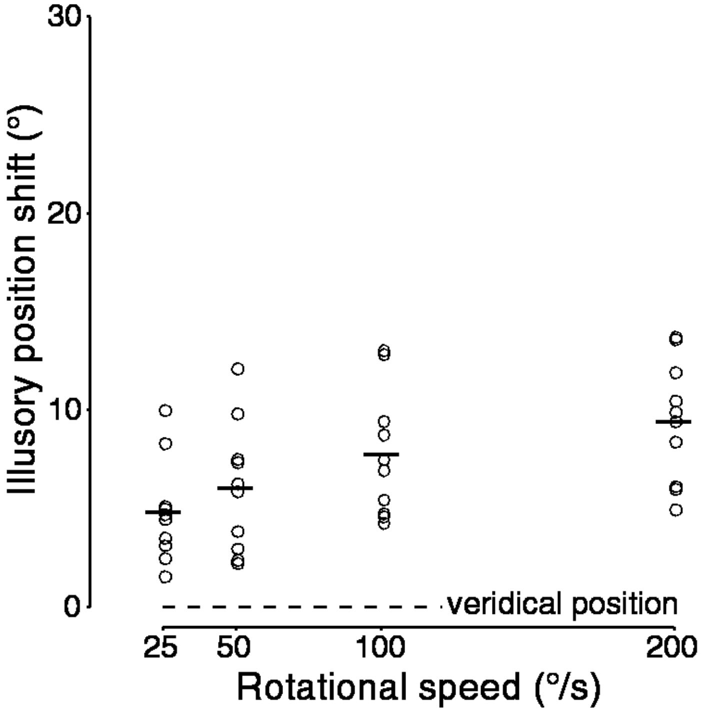

Figure 6. Illusory position shift across rotational speeds in experiment 2 (*n* = 10); same figure format as Figure 3.

Eye velocity traces showed no trend for eye rotation in either of the gratings' two possible rotational motion directions (**Figure 7A**). This is expected because observers did not know which grating was going to be the target when viewing the rotation. We found no consistent torsional eye movements (see **Figure 7B**) and no significant effects of rotational speed on torsional velocity (before reversal: $F(3,27) = 0.57$, $p = .64$, $\eta_g^2 = 0.05$; after reversal: $F(3,27) = 1.14$, $p = .35$, $\eta_g^2 = 0.08$).

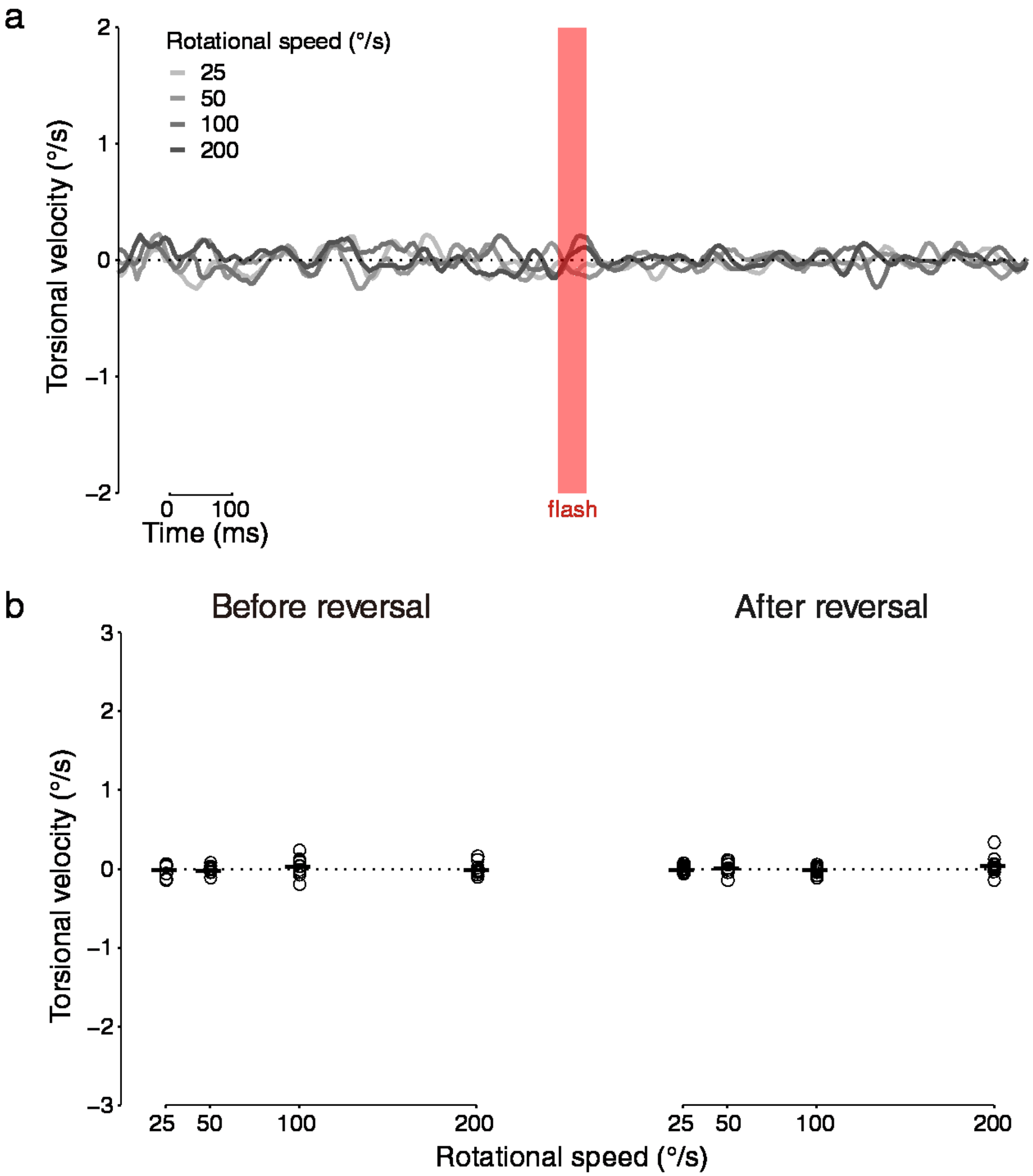

Figure 7. (a) Torsional velocity traces averaged across all observers (*n* = 10) in experiment 2. Figure follows the same format as Figure 4A. (b) Mean torsional velocity for each observer. Figure follows the same format as Figure 4B.

To confirm that the selection of single eye data in each trial did not eliminate any systematic torsional eye movements, we plotted the density of each observer’s torsional velocity (see **Fig. 8a**). This is to examine the possibility that the eyes randomly followed one rotating grating in each trial (i.e., selected one of the two gratings as a target). If the eyes rotated to different directions in each trial, we should expect two peaks in each observer's density plot. However, none of the observers showed two clearly distinguishable peaks, indicating little eye rotations following any particular rotational motion direction. To further confirm that no cyclovergence was induced, we also examined torsional velocity in each eye separately for each participant. Trials were collapsed so that the initial rotational direction of the left stimulus was always CW: if cyclovergence occurred, torsional velocity of the left eye should peak at a positive value before reversal and at a negative value after reversal, and vice versa for torsional velocity of the right eye. However, torsional velocity of both eyes had similar peaks around zero for all participants in all time windows and speeds (**Fig. 8b**). These results indicate that two oppositely-rotating gratings did not induce reliable torsional eye movements. Congruently, we found no correlation between torsional velocity and illusory position shift (before reversal: $r = .09$, $p = .59$; after reversal: $r = -.07$, $p = .68$). Taken together, the persistence of the perceptual illusion and the elimination of consistent torsional eye movements in experiment 2 indicate that there is no causal relationship between torsion and motion perception in the illusion under study.

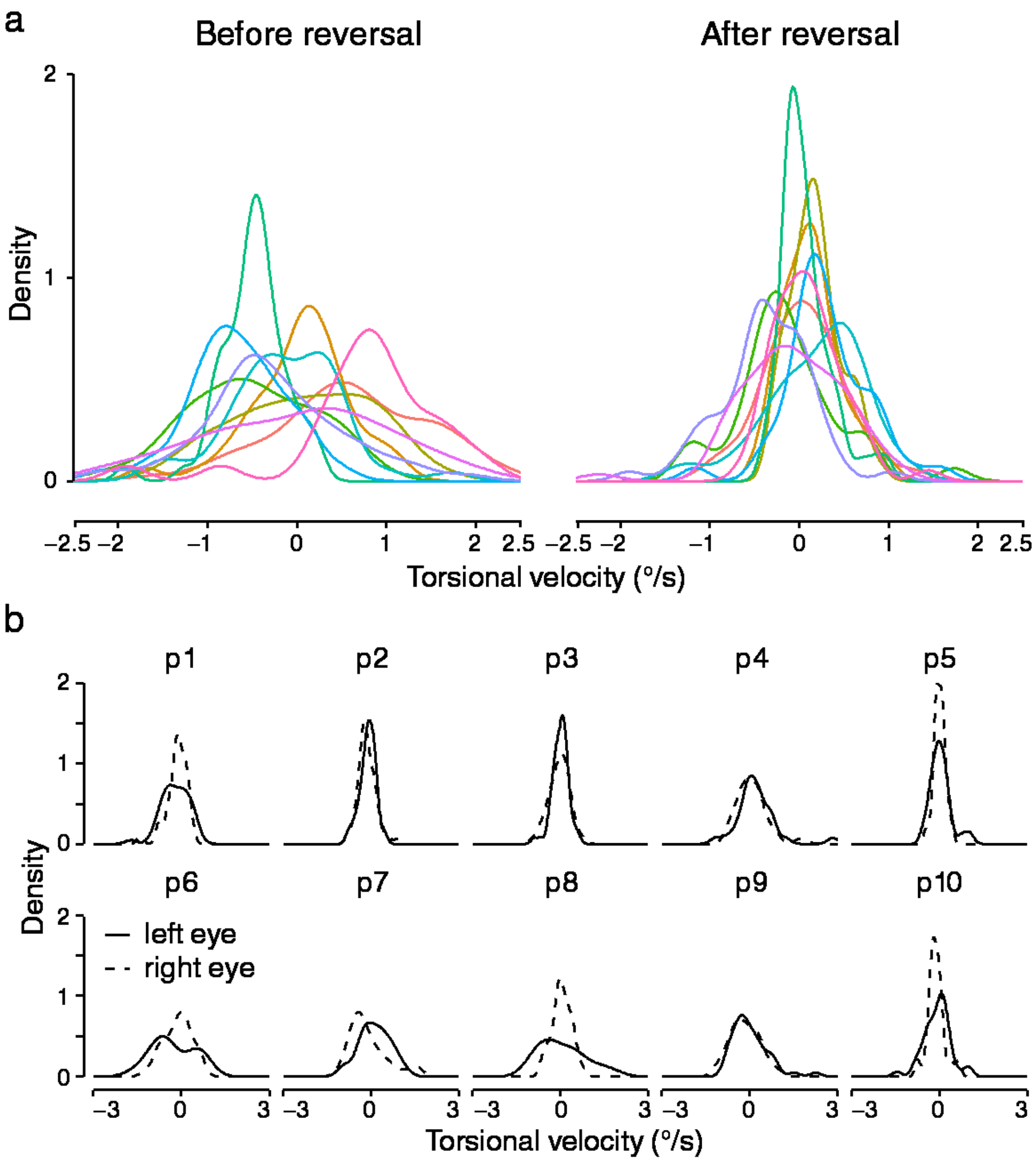

Figure 8. Density of torsional velocity in response to a visual rotational speed of 200°/s in experiment 2. (a) Individual torsional velocity of both eyes in each time window. Each line denotes one participant (*n* = 10). (b) Torsional velocity of each eye in each participant (p1-p10) in the after-reversal time window. Results from other speeds or time windows are similar.

Discussion

Torsional eye rotations are ubiquitous during visual perceptual tasks because they accompany almost every gaze shift. Yet, most experimental studies on perception ignore torsion. Here we used a well-established perceptual illusion, the flash-grab effect, as a test bed for the idea that torsional eye movements interact with visual motion perception. We report two key findings. First, a centrally-presented large-field rotational motion stimulus triggered reliable illusory position shifts and torsional eye movements in the direction of the illusion. Importantly, the magnitude of illusion and torsion were correlated, and both responses scaled similarly with rotational stimulus speed. Second, the perceptual illusion persisted in the absence of systematic ocular torsion. Even though torsion does not cause the perceptual illusion, our findings indicate cross-talk between the perceptual and torsional eye movement system. These results are congruent with studies that have observed similar relationships between illusory motion perception and saccades (van Heusden et al., 2018) or pursuit (Braun, Pracejus, & Gegenfurtner, 2006; Watamaniuk & Heinen, 2007).

The connection between the flash-grab effect and oculomotor responses has previously been shown for saccades. Shifts of the saccadic landing point and the perceived position of the flash were positively correlated across participants, and saccade latency was a good predictor of the size of the perceptual shift (van Heusden et al., 2018). The authors proposed that the close relationship between saccade latency and size of illusion suggests a shared motion-extrapolation mechanism: a corrective signal of the predicted position of the flash stimulus was generated in response to the unexpected motion reversal, which similarly affected planning of saccadic landing point and the shift of perceived position of the flash (Cavanagh & Anstis, 2013; van Heusden et al., 2018). The observed effects on torsion are congruent with these saccade results, and also show that the connection between torsional eye movements and the illusion extends to the after-reversal time window. Since the illusory position shift in the flash-grab effect is mainly driven by motion after the reversal (Blom et al., 2019), the observed correlation in both time windows confirms a tight link between torsion and perception in the flash-grab effect.

In a broader context, our results reveal a close link between visually-induced torsion and motion perception. Previous studies have shown a link between oblique eye position-induced torsion or self-motion induced torsion and perception: the perceived orientation of a line was biased in direction opposite to torsional eye position (Haustein & Mittelstaedt, 1990; Murdison et al., 2017; Nakayama & Balliet, 1977; Wade, Swanston, Howard, Ono, & Shen, 1991). The link between torsion and orientation perception indicates that torsional eye position itself biases perception. In the current study, it remains possible that torsional eye rotation enhances the illusory position shift by causing a bias in orientation perception of the flash. However, testing torsion's contribution to the illusion would require direct manipulation of torsional eye movements, for example by temporally paralyzing extraocular muscles (i.e., the superior obliques) to prevent rotations while observers view and evaluate visual motion. It is also important to note that torsional eye movements are very small rotations of the eye, thus any changes in torsion or its contribution to perception could easily be masked by noise. In seven participants, we attempted to mechanically manipulate torsion by asking them to view the illusion during a 50-deg head tilt, known to induce ocular counter-roll to the opposite direction of the head tilt (Collewijn, Van der Steen, Ferman, & Jansen, 1985; Hamasaki, Hasebe, & Ohtsuki, 2005). We expected that this manipulation would yield a stable counter-roll position and limit any further effects of visual rotational motion on torsion. However, the induction of head tilt did not result in consistent reduction of torsion across participants, probably due to the fact that convergence when viewing a close target reduces ocular counter-roll (Ooi, Cornell, Curthoys, Burgess, & MacDougall, 2004). Instead, head tilt caused larger perceptual noise, thus not allowing us to investigate the limiting effects of abolishing torsion on perception.

Stimulus configurations in experiment 2 eliminated systematic torsional eye movement responses to the illusion, whereas perceptual illusory position shifts persisted. This finding serves as direct confirmation of the previously untested assumption that torsional eye rotations indeed do not cause visual rotational illusions, similar to what has been proposed for the flash-drag effect (Whitney & Cavanagh, 2000), and implied by the fact that the flash-grab effect can occur with translating motion that does not visually induce torsion (Cavanagh & Anstis, 2013; Blom et al., 2019).

Neural correlates of a torsion-perception link

Because torsion and the illusion are induced by rotational motion and are correlated, one possibility is that both systems are triggered by similar input signals. Neurons in the dorsal division of the medial superior temporal area (MSTd) have large receptive fields and are sensitive to rotational motion (Graziano, Andersen, & Snowden, 1994; Mineault, Khawaja, Butts, & Pack, 2012; Tanaka, Fukada, & Saito, 1989). Neurons in this area are also tuned to vestibular rotation signals (Takahashi et al., 2007). There is no direct evidence linking activity in area MSTd to the generation of ocular torsion. However, neurons in cortical motion processing areas such as MSTd project to pontine nuclei in the brainstem and then to cerebellar cortex for the generation of smooth pursuit eye movements. It is therefore possible that similar pathways also connect MSTd with brainstem areas responsible for the generation of torsion, i.e., the rostral interstitial nucleus of the medial longitudinal fasciculus (Leigh & Zee, 2015). Whether motion processing areas such as MST are directly responsible for the generation of motion-induced illusions such as the flash-grab effect is unclear. Human EEG and functional neuroimaging studies suggest that these illusions might be related to activity in the earliest visual cortical areas, predominantly areas V1-V3 (Hogendoorn et al., 2015; Kohler, Cavanagh, & Tse, 2017), but higher-level motion processing areas likely play a role as well. A study using a dichoptic display suggests that the flash-grab illusion might be the manifestation of a hierarchical predictive coding framework, which extends from monocular processing stages (from retina to lateral geniculate nucleus) to binocular processing stages beyond V1 (van Heusden, Harris, Garrido, & Hogendoorn, 2019). It is possible that motion processing signals from MST were obtained by both torsional and perceptual systems, but whereas the perceptual system can use local motion information with opposite motion directions, the torsional system may rely on global motion, yielding the dissociation in experiment 2.

In addition to coding retinal motion, MST also receives extraretinal signals related to eye-in-head movement and directly projects to the frontal pursuit area (FEFsem; Churchland & Lisberger, 2005). These areas might thus play a role in integrating visual and non-visual efference-copy signals (Bakst, Fleuriet, & Mustari, 2017; Nuding, Ono, Mustari, Büttner, & Glasauer, 2008; Ono & Mustari, 2011). Stronger torsional eye movements such as those observed in experiment 1 might trigger a signal boost in areas MST and FEFsem via feedback connections, contributing to the illusion.

In conclusion, similar motion input for torsion and perception and feedback signals could be responsible for the observed relationship between torsional eye movements and perception. Although torsional eye rotations are likely too small to actively trigger a perceptual effect or illusion, they should be taken into account as a factor that may contribute to the strength of a perceptual phenomenon.

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