

On the relation between anticipatory ocular torsion and anticipatory smooth pursuit

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Humans and other animals move their eyes in anticipation to compensate for sensorimotor delays. Such anticipatory eye movements can be driven by the expectation of a future visual object or event. Here we investigate whether such anticipatory responses extend to ocular torsion, the eyes' rotation about the line of sight. We recorded three-dimensional eye position in head-fixed healthy human adults who tracked a rotating dot pattern moving horizontally across a computer screen. This kind of stimulus triggers smooth pursuit with a horizontal and torsional component. In three experiments, we elicited expectation of stimulus rotation by repeatedly showing the same rotation (Experiment 1), or by using different types of higher-level symbolic cues indicating the rotation of the upcoming target (Experiments 2 and 3). Across all experiments, results reveal reliable anticipatory horizontal smooth pursuit. However, anticipatory torsion was only elicited by stimulus repetition, but not by symbolic cues. In summary, torsion can be made in anticipation of an upcoming visual event only when low-level motion signals are accumulated by repetition. Higher-level cognitive mechanisms related to a symbolic cue reliably evoke anticipatory pursuit but did not modulate torsion. These findings indicate that

anticipatory torsion and anticipatory pursuit are at least partly decoupled and might be controlled separately.

Introduction

On the relation between anticipatory ocular torsion and anticipatory smooth pursuit

Real-world movements, ranging from catching prey to hitting a ball, require rapid prediction of an object's trajectory from a brief glance at its motion. It is well-established that smooth pursuit eye movements can be initiated several hundred milliseconds before the onset of object motion, if the direction of the moving target is known in advance (Dodge, Travis, & Fox, 1930; Westheimer, 1954; Boman & Hotson, 1988; Kowler, 1989; Blohm, Missal, & Lefèvre, 2003a,b; Badler & Heinen, 2006; de Hemptinne, Lefèvre, & Missal, 2006; Barnes, 2008; Kowler, 2011; Kowler, Aitkin, Ross, Santos, & Zhao, 2014). These eye movements reflect processes of anticipation of a future motion path, and compensate for sensorimotor delays in situations

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that require fast decisions or actions (Nijhawan, 1994; Wolpert, Ghahramani, & Jordan, 1995; Brenner & Smeets, 2000; Borghuis & Leonardo, 2015).

Anticipatory smooth pursuit eye movements generally occur when target motion is predictable. Such predictions can be based on strong expectations of an upcoming motion direction (Fiehler, Brenner, & Sperling, 2019). At the lowest processing level, these could be induced by repeatedly showing the same kind of stimulus, such as when trials with rightward and leftward target motion are grouped into separate blocks. Stimulus repetition primarily leads to habitual or priming responses through relatively low-level learning processes (Kowler, 1989) in combination with expectation of the upcoming motion based on trial history. Another way of inducing expectation is by presenting targets in a particular configuration that acts as a visual cue, such as when a fixation spot on the left side of the screen will always be followed by rightward target motion. Finally, higher-level symbolic cues have been particularly powerful in eliciting anticipatory pursuit, for example, when a barrier on the left indicates rightward target motion (Kowler, 1989; Kowler et al., 2014). Such symbolic cues can supersede effects of stimulus repetition or simple visual cues (Kowler, 1989; Ladda et al., 2007; Kowler et al., 2014). Different cue types interact differently with the probabilistic information they convey about target motion (Santos & Kowler, 2017). When target motion is entirely unpredictable, anticipatory pursuit can still be based on an estimate of target motion probability, derived from memory and past experience (Heinen, Badler, & Ting, 2005; de Hemptinne, Nozaradan, Duvivier, Lefèvre, & Missal, 2007; Barnes & Collins, 2008; Santos & Kowler, 2017). In summary, anticipatory pursuit eye movements can be driven by a combination of visual and cognitive factors that involve learning of perceptual configurations or simple cues and memory of past history.

A majority of studies on anticipatory smooth pursuit eye movements have used point-like stimuli. However, natural objects may have texture, spatial extent, and rotation around all axes. Such natural objects generate smooth pursuit eye movements that use all three degrees of freedom of the eye's rotation, including a torsional component (rotation about the line of sight). Ocular torsion during pursuit is finely tuned to visual stimulus features such as rotational direction or speed (Edinger, Pai, & Sperling, 2017). However, the properties and neuronal control of pursuit's torsional component are relatively poorly understood.

The current study probes anticipatory torsion by using a stimulus that triggers a horizontal smooth pursuit response with a torsional component. The goal of this procedure is to investigate whether the torsional component of pursuit is decoupled from

or incorporated into the known anticipatory pursuit response. On one hand, torsional eye movements are often considered reflexive, triggered by head roll (Crawford & Vilis, 1991; Demer & Clark, 2005; Hess, 2008) or image rotation (Howard & Templeton, 1964; Cheung & Howard, 1991; Farooq, Proudlock, & Gottlob, 2004; Sheliga, Fitzgibbon, & Miles, 2009; Edinger et al., 2017). On the other hand, there is evidence that torsion is under some level of voluntary control: trained observers can produce it at will (Balliet & Nakayama, 1978), and torsion might be modulated by higher-level mechanisms such as attention (Pashler, Ramachandran, & Becker, 2006; Stevenson, Mahadevan, & Mulligan, 2016). Moreover, torsional eye movements during eye-head gaze shifts seem to anticipate the terminal position of the head after gaze lands on the target, and might thus be driven by a prediction of the gaze (eye-in-head) trajectory (Tweed, Haslwanter, & Fetter, 1998). Together, these findings indicate that torsional eye movements are not purely reflexive, and might be modulated by higher-level processes such as cognitive expectation.

Given the tight behavioral link between horizontal and torsional components of smooth pursuit (Edinger et al., 2017), we hypothesize that a stimulus that moves and rotates in a predictable way will trigger anticipatory pursuit in both the horizontal and torsional direction. In three experiments, we manipulated stimulus predictability via stimulus repetition and configuration (Experiment 1), or different types of symbolic cues (Experiments 2 and 3) to investigate whether horizontal and torsional components of pursuit are affected similarly or differently by these types of predictive signals.

Methods

Observers

We recruited 18 observers (mean age = 25.5, *std* = 4.9 years, seven women) with normal and uncorrected visual acuity (at least 20/20 as assessed using an Early Treatment Diabetic Retinopathy Study (ETDRS) chart) and no history of ophthalmologic, neurologic, or psychiatric disease. Overall, nine observers each were tested in Experiments 1 and 2, and five observers participated in Experiment 3. Four observers, among them authors AR and MS, participated in at least two experiments; their data did not differ systematically from the other observers. The University of British Columbia Behavioral Research Ethics Board approved all experimental procedures, and all observers participated after giving written informed consent.

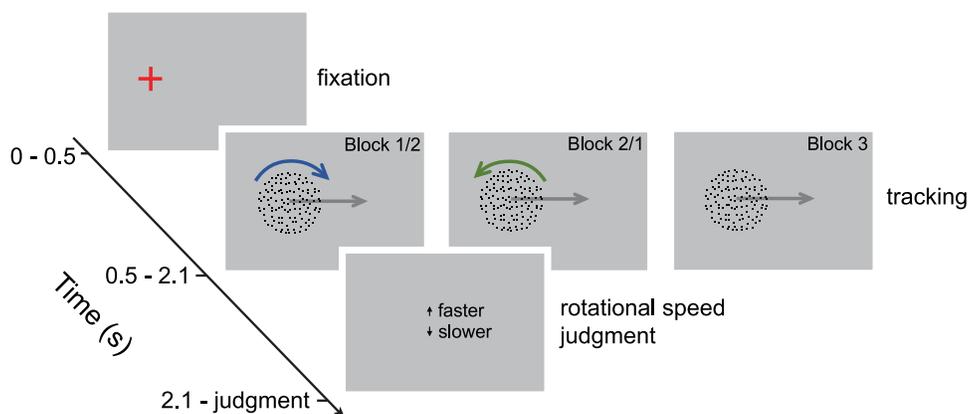


Figure 1. Design and trial timeline in Experiment 1. Each trial began with fixation on a peripheral fixation cross, shown for 450 ms, followed by an interstimulus interval of 50 ms. The rotating target was shown for 1600 ms, followed by a screen prompt to give a perceptual judgment by pressing the up (faster) or down (slower) key on a computer keyboard.

Visual stimuli and setup

Stimuli were random dot patterns (RDP) presented within a disk of 8° diameter on a uniform white background (55 cd/m^2). The RDP consisted of 400 uniformly distributed black dots (0.05 cd/m^2) that were stationary within the disk, each with a diameter of 0.15° . In a given trial, the textured disk moved across the monitor to the left or right at a constant speed of 10 degrees per second ($^\circ/\text{s}$) while rotating around its center in the clockwise (CW) or counterclockwise (CCW) direction at one of five rotational speeds (166, 173, 180, 187, $194^\circ/\text{s}$); rotational speed was manipulated for the purpose of the perceptual task.

Observers viewed stimuli in a darkened room on a gamma-corrected 19-in. CRT monitor set to a refresh rate of 85 Hz (ViewSonic Graphic Series G90fB, 1280×1024 pixels, 36.3×27.2 cm) with a visible range of 37.8° horizontal \times 28.3° vertical from a viewing distance of 55 cm. Each observer's head was stabilized by a bite bar custom-made from dental impression material to reduce motion and instability of the head, and to achieve higher precision in eye tracking. Stimulus and procedure were programmed in MATLAB Version R2015b (The MathWorks Inc., Natick, MA) and Psychtoolbox (Version 3; Brainard, 1997; Pelli, 1997; Kleiner et al., 2007).

Procedure, design, and task

Each block started with a five-point eye-tracker calibration on targets spaced 10° apart on a $20^\circ \times 20^\circ$ grid. In Experiments 1 and 2, trials began with fixation on a red cross (size 1°) at a peripheral location 8° to the left or right of the screen center presented for 450 ms (Figure 1). After a 50-ms interval the RDP

stimulus appeared at the location of the fixation cross and moved across the screen for 1600 ms. The stimulus had the appearance of a rolling ball when rightward translational stimulus motion was combined with CW stimulus rotation (as shown in Figure 1, left), or when leftward translational motion was combined with CCW rotation; we refer to this pattern as “natural” and to the opposite pattern as “unnatural” (shown in Figure 1, middle).

In Experiment 1, horizontal target motion to the right or left was presented in separate blocks of trials. The purpose of this repetition of motion direction within each block was to trigger anticipatory pursuit. Within each series of “left” or “right” blocks, rotational motion direction—either natural or unnatural—was also presented in separate blocks of trials. For example, in a “right natural” block, rightward motion direction was paired with CW rotation; in a “right unnatural” block, rightward motion direction was paired with CCW rotation. The purpose of this was to elicit anticipatory torsion. Order of blocks with stimulus rotation (left, right, natural, or unnatural first) was randomized. In each trial, observers judged whether the rotational speed of the stimulus was faster or slower than the average across all previous trials by pressing an assigned key on a computer keyboard. The purpose of this task was primarily to direct observers' attention to the rotation of the stimulus. The next trial started immediately after the observer indicated their response on the computer keyboard. We also included a baseline condition with rightward or leftward target motion and no rotation (Figure 1, right); these blocks were always presented last. In total, this experiment consisted of six blocks of 200 trials each, run in two separate sessions of no more than 60 minutes each.

In Experiment 2, trials with leftward and rightward translational direction and with natural, unnatural, or no rotation were presented in randomly interleaved

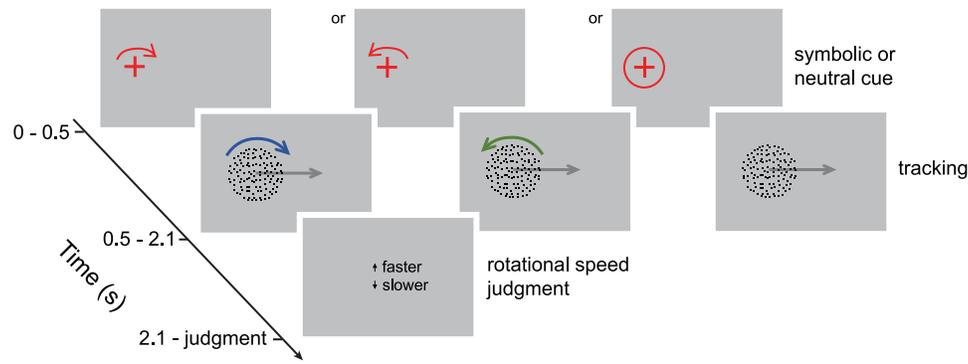


Figure 2. Design and trial timeline in Experiment 2. A symbolic, visual cue was shown during the fixation period, indicating with 100% validity the target's rotation direction in the upcoming trial. Target presentation duration and perceptual task were identical to Experiment 1.

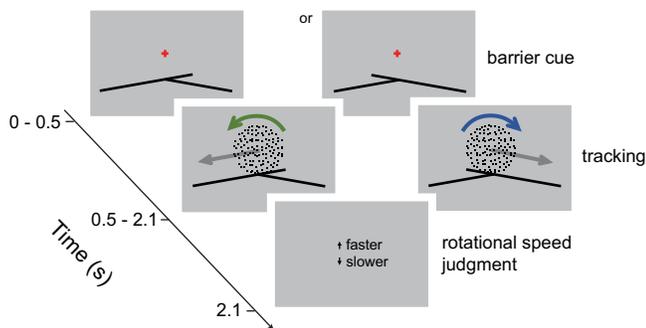


Figure 3. Design and trial timeline in Experiment 3. Following central fixation, the RDP translated down the slope in the motion direction opposite to the indicated barrier. In block 1, the RDP did not rotate, in block 2, a natural rotation direction was always shown. The barrier cue indicated with 100% validity the upcoming target's translational direction in both blocks, and the target's rotational direction in block 2. Target presentation duration and perceptual task were identical to Experiment 1.

order within the same block of trials. Upcoming horizontal direction was 100% predictable based on the location of the fixation cross, that is, fixation on the left was always followed by motion to the right, and vice versa. Upcoming target rotation was indicated by a cue presented above or below the fixation cross for 450 ms. The cue was either an arrow indicating CW or CCW rotational direction, or a noninformative circle around fixation, providing no rotation-directional information (Figure 2). As in Experiment 1, the location of the fixation cross and cue indicated upcoming horizontal target motion reliably (100% validity). This experiment included three blocks of 200 trials each, run in one single 60-minute session.

In Experiment 3, the RDP moved along one of two diagonal line segments that each had a 10° slope (Figure 3). The RDP still translated at the same speed of $10^\circ/\text{s}$, thus the horizontal speed was slightly lower ($9.8^\circ/\text{s}$) than in the other experiments. The fixation cross

was centered at the RDP's start position. In the first block of trials, the RDP moved leftward or rightward with no rotation; in the second block, translational motion was combined with natural stimulus rotation. In both blocks, leftward and rightward motion directions were randomly interleaved. Upcoming target direction was indicated with a 100%-valid barrier cue (4° long extension of the slope above the crossing point) presented from the onset of fixation in all blocks. An extension of the line segment tilted from the upper left to lower right part of the screen, for example, indicated upcoming motion to the right. Each block contained 200 trials, and the experiment was run in one single 30-minute session.

Eye movement recordings and analysis

Eye movements were recorded binocularly with a Chronos ETD (Chronos Vision, Berlin, Germany) at a sampling rate of 200 Hz. This eye tracker is a noninvasive, head-mounted, video-based system that can assess torsional rotations of the eye. It is sufficiently accurate and precise (tracking resolution $<0.05^\circ$ along all three axes) for the fine spatiotemporal analysis of three-dimensional (3D) eye movements. Our procedures for preprocessing and analyzing torsional eye position have been described in Edinger et al. (2017) and are reproduced here in abbreviated form for the readers' convenience.

Three-dimensional eye-in-head position data were processed offline for each eye separately using the Chronos Iris software (Version 1.5) to derive horizontal, vertical, and torsional eye position data from video recordings. The principle of deriving torsional eye position data relies on interframe changes in the iris crypt landmark with each eye rotation. Following standard practice, ocular torsion was obtained from cross-correlation between iris segments across images. Four segments were fitted to each eye's iris and angular

eye position was calculated as a weighted average from all segments with a cross correlation factor of >0.7 . By convention, leftward, downward, and extorsion (i.e., the top of the eye moving away from the nose) of the right eye and intorsion (the top of the eye moving toward the nose) of the left eye are positive.

Eye position data were then analyzed using custom-made routines in MATLAB. Eye position was differentiated to yield 3D eye velocity, and data were filtered using routines described in Edinger and colleagues (2017). Anticipatory pursuit onset was detected in a 100-ms interval around stimulus motion onset by fitting each two-dimensional position trace with a piecewise linear function, consisting of two linear segments (starting 50 ms before onset) and one breakpoint. The least-squares fitting error was minimized iteratively to identify the best location of the breakpoint, defined as the time of pursuit onset. Catch-up saccades occur naturally during pursuit and were identified using a velocity criterion. Eye velocity had to exceed $20^\circ/\text{s}$ in three consecutive frames to be considered a horizontal or vertical corrective saccade and $10^\circ/\text{s}$ to be considered a torsional saccade (backward saccade to reset the eye). Saccade onsets and offsets were defined as the nearest reversal in the sign of acceleration on either side of the three-frame interval. We then computed mean torsional eye velocity and mean horizontal eye velocity in the saccade-free time interval from 50 ms before stimulus onset to 50 ms after stimulus onset, yielding the magnitude of anticipatory torsion and pursuit, respectively.

Manual inspection of each individual eye trace confirmed that the algorithm correctly identified all aspects of horizontal pursuit and torsion; traces with blinks, lost signals, or errors in torsion detection were flagged and excluded from further analysis, resulting in 24.3% excluded trials across observers and experiments. This exclusion rate is owing to the Chronos relying on a clear image of the iris to derive ocular torsion. Any obstruction of the iris due to eyelashes or eye anatomy (e.g., drooping lid) at any time during the trial results in unreliable torsional data, and therefore to rejection of the trial; rejection rates differed between observers and ranged from 4.5% for the most reliable to 43.3% for the least reliable observer. Note that we recorded 3D eye positions from both eyes for each observer. Because the number of usable trials differs between left and right eye for each observer (due to subtle intereye differences in iris shape, structure, and eye lid anatomy), we selected the eye that yielded a larger number of acceptable trials based on torsion data preprocessing for all analyses for each observer.

Statistical analysis

Our experiments were designed to test the following hypotheses: First, we expected that stimulus

configurations in all experiments would reliably trigger anticipatory horizontal pursuit. Second, we hypothesized that all experimental manipulations would also trigger anticipatory torsion because it is closely linked to pursuit. For all experiments, we assessed the effect of rotational motion direction (natural, unnatural, no rotation) on horizontal and torsional eye velocity using repeated-measures analysis of variance (ANOVA) with within-subjects factor *rotation*; we averaged across leftward and rightward horizontal motion directions because we did not expect or observe any horizontal asymmetries. We did not expect anticipatory responses to be modulated by rotational speed, and thus did not include speed in our hypotheses-testing. We further evaluated the relation between anticipatory and visually driven torsional components. Results of the perceptual task are not reported because the purpose of this task was to direct observers' attention to the rotation of the stimulus, and not to assess the relationship between perception and torsion. All reported *t*-tests were two-tailed and, if applicable, Bonferroni-corrected for multiple comparisons. Statistical analyses were conducted in IBM SPSS Statistics Version 23 (IBM Corp., Armonk, NY) and MATLAB Version R2019a (The MathWorks Inc.).

Results

Direction repetition and direction cues reliably trigger anticipatory horizontal pursuit

The stimulus configuration in our paradigm—fixation position to the left or right of screen center combined with centripetal target motion, or the presence of the barrier cue—made the target's horizontal motion direction predictable. As a result, observers reliably initiated anticipatory horizontal pursuit in the direction of the upcoming target, starting on average 200 ms before motion onset in both experiments. These findings are demonstrated in mean horizontal eye velocity traces for all three experiments (Figure 4). Interestingly, in Experiment 1, anticipatory horizontal pursuit velocity differed depending on whether the stimulus rotated or not (Figure 4b). This observation was confirmed by a main effect of *rotation* on anticipatory pursuit velocity, $F(2, 16) = 25.26$, $p < 0.001$, $\eta^2 = 0.76$. Anticipatory pursuit velocity was significantly reduced in comparison to the no-rotation baseline when the stimulus rotated naturally [$t(8) = 7.27$, $p = 0.02$] and unnaturally [$t(8) = 6.83$, $p = 0.01$]. Even though the magnitude of anticipatory pursuit velocity was comparable across experiments [Experiment 1: $M = 1.74^\circ/\text{s}$, $std = 0.72$; Experiment 2: $M = 1.95^\circ/\text{s}$, $std = 1.04$; Experiment 3: $M = 1.45^\circ/\text{s}$,

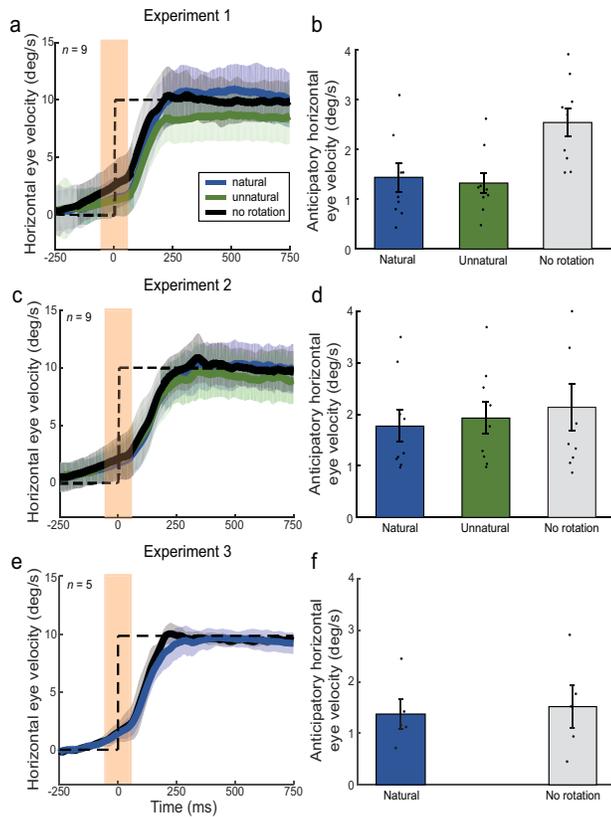


Figure 4. Horizontal smooth pursuit eye movements in response to anticipated and visual target motion. (a,c,e) Mean horizontal eye velocity traces in Experiments 1 ($n = 9$), 2 ($n = 9$), and 3 ($n = 5$). Shaded areas denote between-subject standard deviations. (b,d,f) Mean anticipatory horizontal eye velocity in the interval from 50 ms before to 50 ms after target motion onset; each data point indicates the mean for one observer in Experiment 1, 2, and 3. Error bars denote standard error of the mean.

$std = 0.78$; $F(2, 20) = 0.53$, $p = 0.60$, $\eta^2 = 0.05$], it did not depend on stimulus rotation in Experiments 2 and 3. These observations are confirmed by a lack of significant main effect of rotation for Experiment 2 (natural vs. unnatural vs. no rotation; $F(2, 16) = 2.03$, $p = 0.19$, $\eta^2 = 0.20$), and Experiment 3 (natural vs. no rotation; $F(1, 4) = 0.70$, $p = 0.45$, $\eta^2 = 0.15$).

Only stimulus repetition, not symbolic cues, elicit anticipatory torsion

Importantly, we found that observers anticipated the target's rotational direction. The eyes rotated about the visual axis either CW in response to “natural” or CCW in response to “unnatural” rotation prior to target onset. Figure 5a shows mean torsional velocity traces for Experiment 1, revealing a separation of responses to natural versus unnatural rotation several

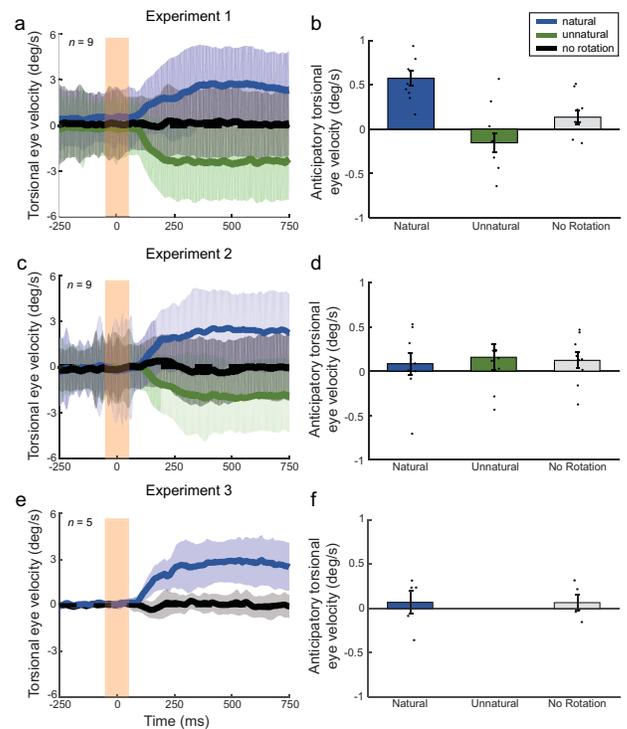


Figure 5. Torsional eye movements in response to anticipated and visual target rotation. (a,c,e) Mean torsional eye velocity traces in Experiments 1, 2, and 3, following the same conventions as in Figure 4. (b,d,f) Average anticipatory torsional eye velocity in Experiments 1, 2, and 3.

hundred milliseconds prior to target motion onset. These observations are reflected in comparisons of mean torsional eye velocity during the same interval as anticipatory smooth pursuit, from 50 ms before to 50 ms after target onset, in Experiment 1 (Figure 5b). Rotational direction had a significant main effect on mean anticipatory torsional velocity, $F(2, 16) = 14.6$, $p < 0.005$, $\eta^2 = 0.65$, mostly driven by the difference between natural rotation and no rotation [$t(8) = 3.94$, $p < 0.004$]. The difference between unnatural rotation and the no-rotation baseline was nonsignificant when corrected for multiple comparisons [$t(8) = 2.21$, $p = 0.15$] because mean anticipatory torsion was overall weaker in response to unnatural rotation. These findings indicate that anticipation of rotational motion direction, triggered by stimulus repetition, can modulate ocular torsion, especially in response to a naturally rotating stimulus that causes stronger torsion overall (Figure 6a). By contrast, cognitive expectation triggered by a symbolic cue did not modulate ocular torsion, regardless of whether this cue was paired with a particular stimulus configuration (location of the fixation cross as a stationary visual cue, Experiment 2) or whether it was used in isolation (Experiment 3). Results from these two experiments reveal no anticipatory torsion (Figure 5c,e) and no

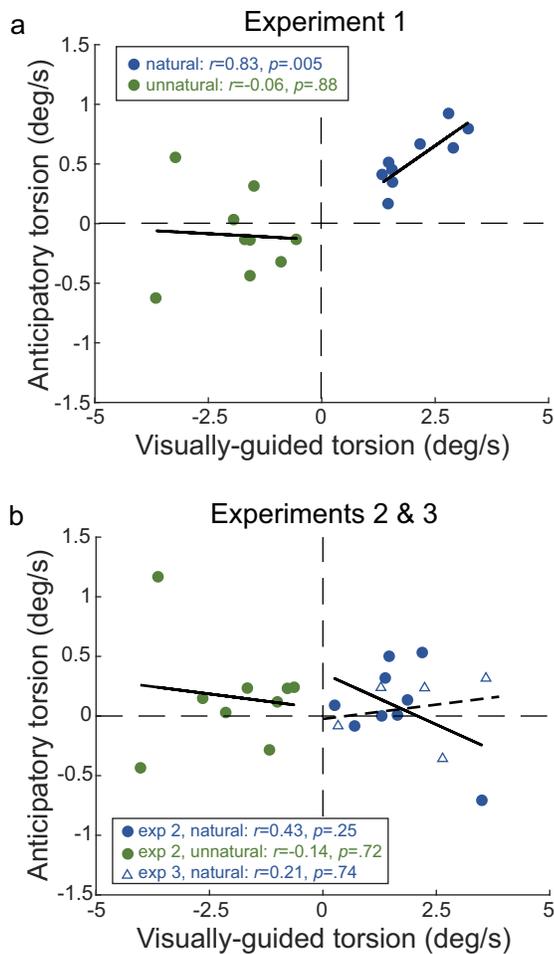


Figure 6. Comparison of the magnitude of visually guided torsion and anticipatory torsion in (a) Experiment 1 and (b) Experiments 2 and 3. Black lines indicate best-fit linear regressions. Each data point represents the mean for one observer.

significant main effect of rotational direction (natural, unnatural vs. no rotation in Experiment 2, or natural vs. no rotation in Experiment 3) on torsional velocity (Figure 5d,f; both $F < 1$). Although the magnitude of anticipatory torsion in Experiment 1 was correlated with the magnitude of visually guided torsion, there was no such relationship between anticipatory and visually guided torsion in Experiments 2 and 3 (Figure 6b).

Disentangling the effects of short-term and long-term expectation

The results described so far are based on averages across all trials in a given block. We next investigated how anticipatory pursuit and anticipatory torsion built up over the course of a block of trials, and compared the temporal development for anticipatory pursuit and torsion. Figure 7 shows anticipatory eye velocity

accumulated over time, that is, eye velocity at trial = 1 is the anticipatory eye velocity in trial 1 for all observers; eye velocity at trial = 10 is the eye velocity averaged across trials 1-10 for all observers. In Experiment 1, anticipatory pursuit responses built up quickly within the first five trials (Figure 7a). Accumulation profiles were similar in all conditions, despite differences in anticipatory pursuit magnitude (see Figure 7c,e). In Experiment 2, anticipatory pursuit built up faster in trials in which the stimulus rotated as compared with no-rotation trials (Figure 7c), possibly indicating the cost of decoding the neutral cue in that condition. In Experiment 3, anticipatory pursuit built up more slowly than in Experiments 1 and 2 (Figure 7e), possibly because the translational direction in Experiment 3 was only indicated by the barrier cue, not by an additional stationary cue (location of fixation spot).

The temporal development of anticipatory torsion in Experiment 1 was slower than for anticipatory pursuit; anticipatory torsion took approximately 20 trials to reach its maximum (Figure 7b). There was no notable change in the anticipatory torsional velocity response in Experiment 2 (Figure 7d) or in Experiment 3 (Figure 7f). The comparison between anticipatory pursuit and torsion in Experiment 1 indicates that low-level visual signals derived from stimulus repetition or priming drives both responses, but at a different temporal rate.

To isolate the effect of longer-term cognitive expectation, we randomized the order of motion directions in Experiments 2 and 3. However, it is still possible that short-term priming effects might have occurred due to recent trial history (Kowler, 1989; Heinen et al., 2005). To investigate the effect that the preceding trials might have had on anticipatory pursuit and torsion in a given trial, we conducted a tree-plot analysis for pursuit and torsion in those blocks in Experiments 2 and 3, in which translational or rotational directions were randomized. In Figure 8, we show averaged eye velocities in trial n as a function of rotational (or translational) direction in the previous two trials ($n-1$ and $n-2$). If a priming effect existed for torsion, for example, we would expect eye velocity of trials preceded by a stimulus with CW rotation to be more positive than the averaged eye velocity of trials preceded by CCW rotation. We observed no systematic priming effect for either torsion in Experiment 2, or torsion or pursuit in Experiment 3, when averaging data across all participants. However, some individual observers' data reflect effects of priming. We conducted two-way ANOVAs (factor 1: direction of current trial; factor 2: direction of previous trial; test effect of factor 2) on individual observer data, revealing significant trial history effects for zero out of nine observers' torsion in Experiment 2, two out of five observers' torsion in Experiment 3, and zero out of five observers' pursuit in Experiment 3. However, given that the majority of

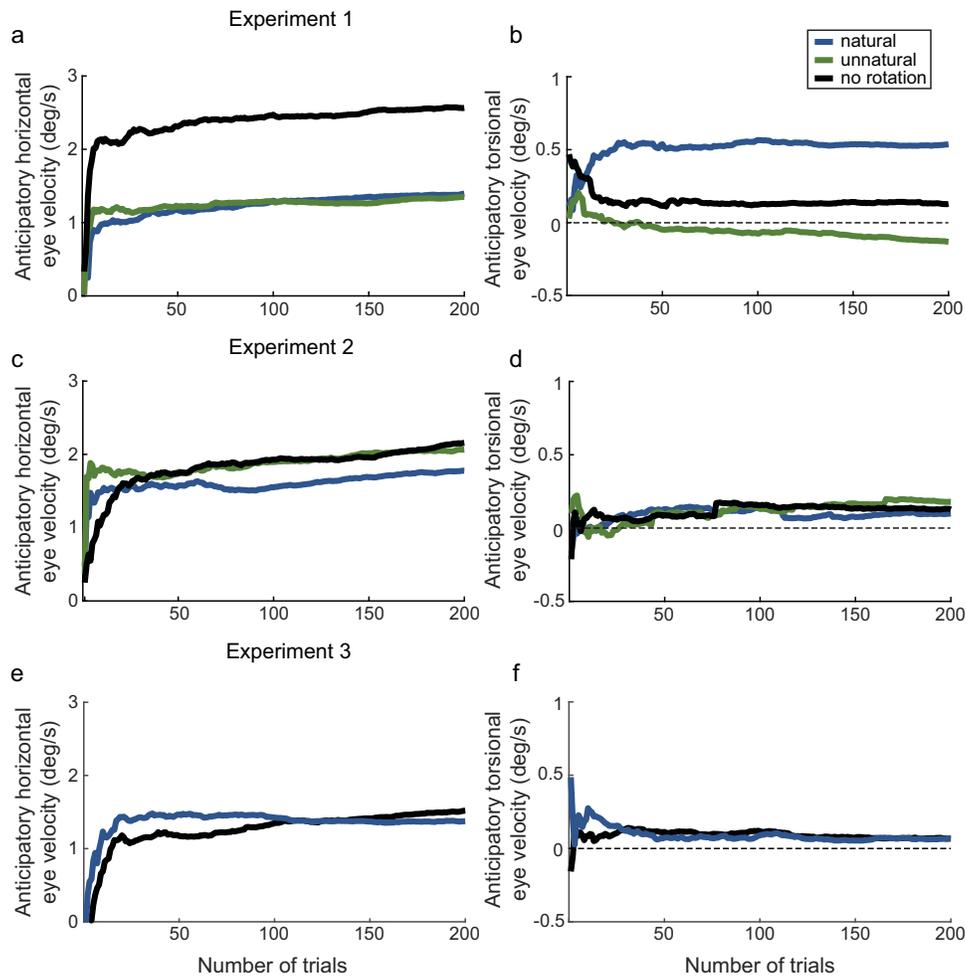


Figure 7. Cumulative anticipatory eye velocities across observers (panels a–d show averages for $n = 9$, panels e and f show averages for $n = 5$). (a,c,e) Anticipatory horizontal eye velocity in Experiments 1, 2 and 3. (b,d,f) Anticipatory torsion in Experiments 1, 2, and 3.

observers did not exhibit trial history effects, and that the overall magnitude of anticipatory torsion was very small, it is unlikely that priming played a significant role in driving anticipatory eye movements in these two experiments.

Discussion

In 1989, Eileen Kowler published a seminal article in which she demonstrated convincingly that “anticipatory smooth eye movement depended on both the cognitive expectations about the direction of future target motion and on the recent past history of stimulus motions” (Kowler, 1989; p. 1055). Kowler’s early findings attributed anticipatory pursuit to cognitive expectations, showing that simple oculomotor learning was insufficient to explain smooth movements of the eye prior to target motion onset. These results had significant ramifications for how we view smooth

pursuit eye movements: not only as the retinal-slip driven visual response tightly linked to low-level motion processing, but also as a sensitive read-out of higher-level cognitive processes, such as predictive motion signals (Barnes, 2008; Kowler, 2012; Kowler et al., 2014).

Here we show that anticipatory ocular torsion can be elicited prior to the onset of a moving and rotating visual stimulus. However, whereas anticipatory pursuit was elicited reliably across experiments employing different cue strengths, anticipatory torsion was only triggered if the same pattern of rotational motion was presented repeatedly. This anticipatory response is therefore more likely to be driven by low-level learning or adaptive processes, and not by higher-level cognitive processes. Symbolic cues, such as arrow cues (Experiment 2) or barrier cues (Experiment 3) indicating an upcoming direction, require conscious higher-level decoding of the cue’s meaning—a cognitive process that appears to be decoupled from the control of ocular torsion. The cues’ differential potential in

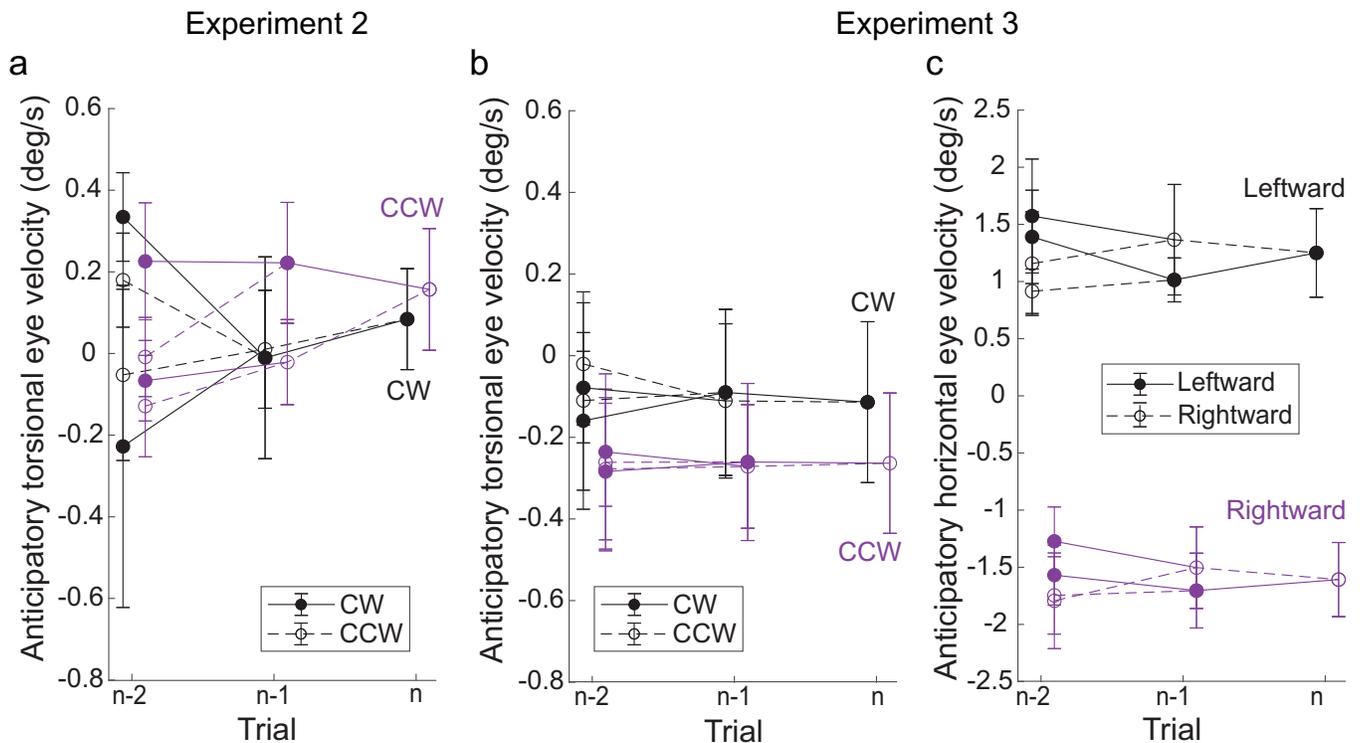


Figure 8. The effect of previous trials on torsional anticipatory eye velocity when rotational or translational directions were randomized. The knot for trial n represents averaged eye velocity across all trials in which the stimulus rotated in a given direction (CW: black; CCW: purple) or translated in a given direction (left: black; right: purple). Moving to the left along the x axis, the two knots for trial $n-1$ show the averaged eye velocity of trials split by the direction of the preceding trial, and so on. (a) Mean anticipatory torsion in Experiment 2 ($n = 9$). (b) Mean anticipatory torsion and (c) mean anticipatory horizontal pursuit in Experiment 3 ($n = 5$). Error bars denote standard error of the mean.

driving anticipatory pursuit and torsion indicates that these two types of anticipatory responses are at least partly decoupled and controlled separately.

There are several preliminary findings in the literature indicating that torsion might be under cognitive control, and our findings are in conflict with these reports.

Balliet and Nakayama (1978) report that torsional eye movements can be produced at will and initiated in the complete absence of a vestibular or visual stimulus. This finding indicates the plasticity of the torsional system and its capacity for learning. However, these results were obtained in only three subjects and after many hours of training. Pashler and colleagues (2006) found that the eyes produced ocular torsion when a large sample of observers ($n = 33$) attended to a five-letter word rotated CW or CCW by 15° to 45° . It is important to note that torsion was not directly assessed in this study. Instead, observers were asked to adjust a reference line to match the tilt of an afterimage produced by the rotated word; tilt of the reference line was taken as evidence that the eye must have rotated. Stevenson and colleagues (2016) assessed ocular torsion using scleral search coils (an invasive technique with high accuracy and precision) in response to a rotating stimulus that

contained different frequency components in the center and periphery. The authors show that cyclovergence (when both eyes rotate in the same direction) was modulated by attention, that is, higher-amplitude torsion in the direction of the attended versus the unattended frequency component. This effect was present in average results for six observers, but was based on attentional modulation found in only three observers; the other three observers' torsion was not or only mildly modulated by attention. Taken together, these three studies indicate that sustained torsional eye movements might be influenced by cognitive factors, but these reports require replication with larger sample sizes or detailed eye movement measurement.

Our results are consistent with the view that torsional eye movements are not purely reflexive or the mere byproduct of a gaze shift, as originally indicated by Donders' and Listing's law. Instead, torsion might be susceptible to learning or adaptation to a given rotational motion direction. Yet, in comparison with anticipatory horizontal pursuit, anticipatory torsion does not seem to be under much cognitive control. Anticipatory smooth pursuit is commonly associated with activity in frontal brain areas, such as

the frontal eye fields (Macavoy, Gottlieb, & Bruce, 1991; Fukushima, Yamanobe, Shinmei, & Fukushima, 2002), and in particular with the supplementary eye fields (Heinen & Liu, 1997; Missal & Heinen, 2004; Kim, Badler, & Heinen, 2005). However, there is no direct evidence that signals from these frontal cortical brain areas directly mediate the descending signals to the brainstem and cerebellum that are well-known to guide ocular torsion.

Our findings also indicate a link between horizontal and torsional components of pursuit. Observers in our study initiated horizontal pursuit up to 200 ms prior to stimulus motion onset. This effect was stronger for baseline (no rotation) than for rotation conditions in Experiment 1, indicating that the pursuit system takes torsional eye rotation into account when computing anticipatory horizontal pursuit velocity. Our Experiments 2 and 3 provided further evidence for this link by showing similar magnitude of anticipatory pursuit across conditions in the absence of anticipatory torsion. By contrast, Murdison, Paré-Bingley, and Blohm (2013) showed that eye movement signals that result from ocular counterroll during head rotation were not taken into account when making an anticipatory pursuit movement. These authors conclude that ocular torsion is not integrated with velocity memory signals. There are several important differences between Murdison and colleagues' (2013) paradigm and our present study that could explain this discrepancy. Although torsion and pursuit were elicited by different signals in the Murdison study—vestibular signals for torsion and visual signals for pursuit—both response components were driven by the same visual stimulus in our study, resulting in torsional velocity integration in pursuit.

It is noteworthy that these integration effects were observed despite the small magnitude of torsion in general, and of anticipatory torsion in particular. Visually induced torsion typically has a gain of <0.1 (Sheliga et al., 2009), similar to what we observed here. Yet, these tiny responses appear to impact anticipatory horizontal pursuit, and might contribute to the perception of rotational motion illusions (Wu & Spering, 2019).

Limitations

The interpretation of our findings is limited by several factors, most notably by the small magnitude of the movement under study, and by the overall small effect sizes, even when anticipatory torsion was elicited in Experiment 1. Because of this, some experimental manipulations are not feasible. For example, it would be interesting to present moving stimuli with completely randomized translational and rotational motion directions, without a cue, to examine the isolated

effects of trial history as has been done in the past for anticipatory pursuit (Kowler, 1989; Heinen et al., 2005). Yet, even a highly salient barrier cue did not reliably trigger anticipatory torsion in our experiments, rendering it unlikely that anticipatory torsion would survive complete randomization.

Further, it is noteworthy that the onset of anticipatory torsion in Experiment 1 was very early. A difference between conditions could already be observed 200 ms before stimulus onset, prior to the onset of anticipatory pursuit. It is possible that torsional anticipation was not strictly time-locked to the stimulus onset, but resulted from a shift in baseline torsional activity in preparation of the upcoming stimulus. We cannot rule out this alternative explanation, although it is interesting that there was no such early baseline activity in Experiments 2 and 3. Notwithstanding the possibility of this alternative explanation, it is important to note that even a potential shift in baseline torsion occurred prior to stimulus onset, and can therefore be interpreted as being part of an anticipatory response.

Conclusion

Taken together, our results emphasize important differences and similarities between the pursuit and the torsional system. Smooth pursuit eye movements are visually induced but can be modulated by a large number of cognitive factors, such as expectation, attention, and reward (Barnes, 2008). Torsional eye movements, although susceptible to habit or potentiation due to trial sequence, appear less cognitively controlled. These findings have important implications for our understanding of the brain mechanisms underlying the integration of both responses, as well as the impact of these eye movements on visual perception.

Keywords: anticipation, cognitive expectation, ocular torsion, prediction

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