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Eye movements during optic flow perception

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ABSTRACT

Optic flow is an important visual cue for human perception and locomotion and naturally triggers eye movements. Here we investigate whether the perception of optic flow direction is limited or enhanced by eye movements. In Exp. 1, 23 human observers localized the focus of expansion (FOE) of an optic flow pattern; in Exp. 2, 18 observers had to detect brief visual changes at the FOE. Both tasks were completed during free viewing and fixation conditions while eye movements were recorded. Task difficulty was varied by manipulating the coherence of radial motion from the FOE (4 %-90 %). During free viewing, observers tracked the optic flow pattern with a combination of saccades and smooth eye movements. During fixation, observers nevertheless made small-scale eye movements. Despite differences in spatial scale, eye movements during free viewing and fixation were similarly directed toward the FOE (saccades) and away from the FOE (smooth tracking). Whereas FOE localization sensitivity was not affected by eye movement instructions (Exp. 1), observers' sensitivity to detect brief changes at the FOE was 27 % higher (p <.001) during free-viewing compared to fixation (Exp. 2). This performance benefit was linked to reduced saccade endpoint errors, indicating the direct beneficial impact of foveating eye movements on performance in a fine-grain perceptual task, but not during coarse perceptual localization.

1. Eye movements during optic flow perception

Optic flow is generated when we move through a largely stationary environment. It is defined by the apparent motion of objects relative to the observer, and is used across species as an important visual cue for navigation (Gibson, 1950; Baird et al., 2021). When we locomote through our environment, optic flow helps maintain balance, posture and gait stability (Lestienne, Soechting, & Berthoz, 1977; Prokop, Schubert, Berger, 1997; Warren, Kay, Zosh, Duchon, & Sahuc, 2001). Optic flow also informs perceptual tasks, such as judging heading direction (Warren & Hannon, 1988; Lappe, Bremmer, & van den Berg, 1999), estimating travel distance (Bremmer & Lappe, 1999; Bury, Jenkin, Allison, & Harris, 2020; Redlick, Jenkin & Harris, 2001), and steering (Alefantis, Lakshminarasimhan, Avila, Noel, Pitkow, & Angelaki, 2022). During these types of tasks, observers can be expected to move their eyes freely and incessantly to bring objects of interest close to the fovea. A combination of foveating eye movements such as saccades, smooth pursuit, and fixation may serve perceptual stability during self-motion (Lappe, Pekel, & Hoffman, 1998; Niemann, Lappe, Büscher, & Hoffmann, 1999; Knöll, Pillow, & Huk, 2018; Chow, Knöll, Madsen, & Spering, 2021; Piras, Raffi, Persinani, Perazzolo, & Squatrito, 2016; Raffi, Trofè, Perazzolo, Meoni, & Piras, 2021).

However, the role of eye movements in perceptual tasks related to optic flow is unclear and there is evidence for both perceptual benefit and bias resulting from eye movements. Eye movements are linked to perceptual performance benefits in tasks involving visual motion. For example, engaging in smooth pursuit eye movements as compared to fixating on a target improves motion prediction through the availability of extraretinal cues (efference copy or proprioceptive inputs; Bennett, Baures, Hecht, & Benguigui, 2010; Spering, Schütz, Braun & Gegenfurtner, 2011). This benefit extends across stimuli and modalities, such as when predicting the trajectory of a target that is temporarily occluded (Becker & Fuchs, 1985; Barnes, 2008) or when manually intercepting a moving object (van Donkelaar, Lee & Gellman, 1994; for reviews see Fiehler, Brenner, & Spering, 2019; Fooken, Kreyenmeier, & Spering, 2021). Eye movement manipulations can also induce bias in motion perception. For example, manipulating the direction of saccades (backward vs forward) at the onset of smooth pursuit biases speed

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perception (slower vs faster) compared to trials without saccades (Goettker, Braun, Schütz, & Gegenfurtner, 2018; Goettker & Gegenfurtner, 2021). The present study is based on the idea that eye movements affect how we perceive and interact with visual motion and investigates the interaction between eye movements and the perception of optic flow direction.

On one hand, we might expect to see performance benefits. For example, the perception of optic flow direction in a simulated heading task was better when observers tracked a target moving horizontally across the midline by actually executing an eye movement compared to when they fixated and the consequences of this eye movement were merely simulated (Royden, Banks, & Crowell, 1992; Crowell, Banks, Shenoy, & Andersen, 1998; see review by Lappe et al., 1999). Because the tracking and fixation conditions yielded the same retinal image motion, these studies suggest that observers are able to extract and utilize extraretinal cues for accurate heading judgments. These behavioral findings are paralleled by neurophysiological results indicating that the tuning of heading direction in motion-sensitive medial superior temporal area (MST) and ventral intraparietal area (VIP) takes pursuit into account (e.g., Page & Duffy, 1999; Maciokas & Britten, 2010, Manning & Britten, 2019) and represents heading direction in eye-centered coordinates (Lee, Pesaran, & Andersen, 2011). Moreover, real-world eye-movement studies have identified intermittent sampling of the scene and look-ahead fixations in uninstructed observers during driving (e.g., Mourant & Rockwell, 1972; Lappi, Rinkkala & Pekkanen, 2017). The authors speculate that such natural gaze behavior might serve to maintain and update scene layout across saccades. Similar look-ahead behavior was observed during natural walking across multiple terrains, indicating that eye movements might be used optimally, and therefore should be beneficial, in helping observers navigate across environments with different complexity and demands (Matthis, Yates, & Hayhoe, 2018).

On the other hand, there is evidence for performance similarity during tracking compared to fixating (Warren & Hannon, 1990), or for performance impairments. For example, when observers make saccades while judging heading direction, judgments are compressed toward straight ahead during the saccade (Bremmer, Churan, & Lappe, 2017), in line with findings that space is compressed at around the time of a saccade (Morrone, Ross, & Burr, 1997). These findings suggest that executing saccades while estimating heading direction can lead to systematic misperception.

The present study aimed to investigate the effect of different types of naturally-occurring eye movements on localizing the focus of expansion (FOE) in an optic flow pattern, a task that relies on perceiving the direction of the dots in the flow field. In order to evaluate the relationship between eye movements and optic flow direction perception across task demands, observers performed two different tasks during free viewing and fixation. They either had to spatially localize the FOE on a coarse spatial scale (Exp. 1) or perform an additional sensitivity task at the FOE location on a finer spatial scale (Exp. 2), presumably requiring foveal vision. We hypothesized that eye movements would intuitively track the FOE in replication of our previous findings (Chow et al., 2021), and that this would hold across eye movement type and spatial scale (i.e., for smooth tracking movements, saccades, and microsaccades). Second, we hypothesized that executing an eye movement (a saccade toward the FOE or tracking of dot motion) would benefit optic flow direction perception, in line with studies finding pursuit benefits in similar tasks (Royden et al., 1992). Congruently, we expected that eye movement direction should be linked to perceptual accuracy on a trial-by-trial basis.

2. Experiment 1: FOE coarse localization

2.1. Method

2.1.1. Participants

Twenty-three adults (18 female; mean age $M = 25.8$ yrs; $SD = 5.9$ yrs) with normal or corrected-to-normal visual acuity participated in this experiment. Sample size was larger than in previous studies comparing the influence of eye movement instructions on perceptual performance (e.g., Crowell & Banks: max. $n = 3$; Royden et al., 1992: $n = 4$; Warren & Hannon, 1990: max. $n = 8$). The experimental procedures adhered to the Declaration of Helsinki and were approved by the Behavioral Research Ethics Board of the University of British Columbia. All participants provided written informed consent before participation and received CAD 10 per hour of participation as remuneration.

2.1.2. Visual display, stimuli and apparatus

Participants sat at a distance of 60 cm from a computer monitor (NEC FP2141SB; 36.0° × 28.1°; resolution 1600 × 1200 pixel; refresh rate 85 Hz) where visual stimuli were presented. Participants were asked to rest their head against a combined chin and forehead rest to minimize head movements. Visual stimuli were generated using MATLAB R2018b (The MathWorks Inc., Natick, MA) and Psychtoolbox v. 3.0.12 (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007). Dots (diameter = 0.1°, lifetime = 47 ms, luminance = 94.0 cd/m^2, Michelson contrast = 46 %) were presented in a rectangular aperture of 29.0° (width) × 22.2° (height) at a density of 0.4 dots/deg^2 against a grey background with luminance 35.0 cd/m^2 (Fig. 1**A**). A portion of dots was designated as signal dots, whose motion direction and velocity were determined based on the distance between the dot location (x) and the FOE location (x_{FOE}), multiplied by the distance ratio (virtual depth / $z_{FOE} = 2$ m for all dots; translational speed / $\dot{z} = 2$ m/s). Specifically, the dot velocity was determined using the formula below (shown for horizontal direction, same for vertical dimension):

$$\dot{x} = (x_{FOE} - x) \times \frac{\dot{z}}{z_{FOE}}$$

The remaining dots were designated as noise dots and moved in random directions. The percentage of signal dots to noise dots was termed motion coherence, presented at levels of 4 %, 8 %, 16 %, 32 %, or 64 % (where 100 % would indicate that all dots move in the same direction). When a dot reached its lifetime or moved outside of the stimulus aperture, the dot was redrawn at a random location within the aperture and its signal/noise identity was reassigned. The focus of expansion of the optic flow pattern (FOE) was placed at one of twelve possible locations distributed across four quadrants at a distance of 6.6° from the central fixation point (Fig. 1**B**).

During the fixation condition, a fixation cross was presented in the screen center throughout each trial. The fixation target was composed of a cross hair (width = 0.2°) on top of a bull's eye (diameter = 0.6°), which has been shown to induce accurate fixation (Thaler, Schütz, Goodale, & Gegenfurtner, 2013). Eye positions were recorded at 1000 Hz sampling rate (monocular, right eye) using an Eyelink 1000 Plus (SR Research, ltd., Kanata, ON, Canada).

2.1.3. Procedure

During optic-flow stimulus presentation, participants either received no instruction about what to do with their eyes (free-viewing condition), or they were asked to maintain fixation on the fixation cross (fixation condition). If participants moved their eyes more than 1° away from the fixation location, they received feedback to maintain fixation, and the respective trials was later discarded.

Each trial started with a central fixation cross, which remained on screen throughout the trial in the fixation condition, and was removed during free viewing. After the eye tracker performed a drift correction, the optic flow stimulus was presented for 1 s. Participants then

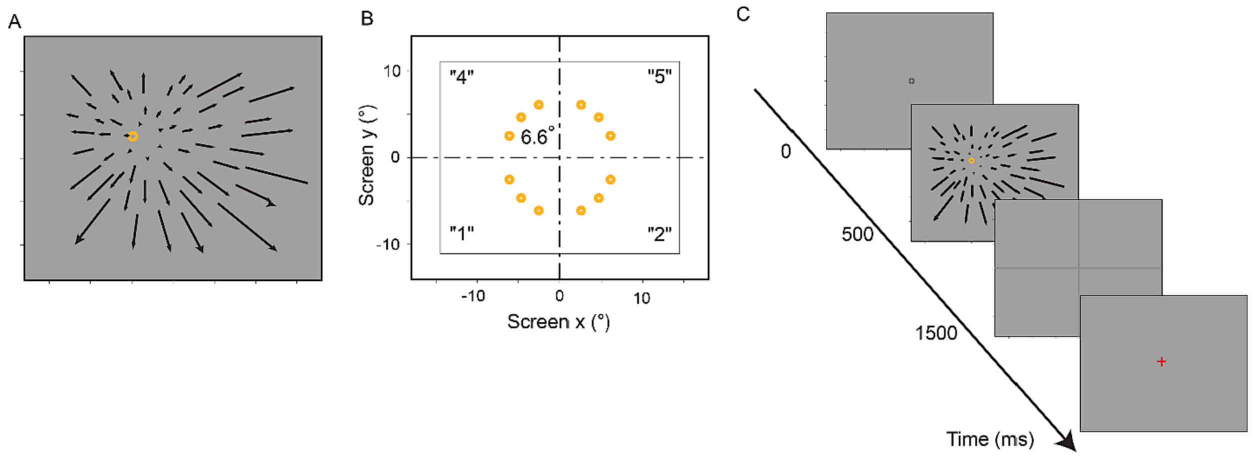

Fig. 1. (A) Optic flow stimulus display. Arrows indicate dot motion direction and speed (the longer the line, the higher the dot velocity at a given location), originating from the FOE (orange circle; not shown to observer). (B) Illustration of possible FOE locations (orange circles) with respective button press instructions (shown only for illustration purposes); grey rectangle indicates the extent of the dot display, denoted in degrees of visual angle. (C) Trial timeline.

performed a 4-alternative forced-choice (4AFC) task to judge which of the four quadrants contained the FOE by pressing the corresponding button on the computer keyboard's number pad (e.g., "4" for the top-left quadrant; Fig. 1**B**). After judgment, the central fixation cross changed color for one second and turned green to indicate a correct response and red to indicate an error (Fig. 1**C**).

Participants completed 24 trials for each of the five motion coherence levels, yielding a total of 120 trials per eye movement condition. Motion coherence was randomized within each block of trials, and eye movement instructions were blocked; the order of eye movement instruction was counterbalanced across participants. Including breaks between blocks, the experiment took no more than 60 min to complete.

2.1.4. Eye movement data preprocessing and analysis

In both experiments, the presented optic flow pattern naturally elicited different types of eye movements: saccades and smooth tracking movements, which bear resemblance to the characteristics of smooth pursuit initiation, but occur involuntarily and could not easily be suppressed (i.e., they were visible regardless of eye movement instruction). We therefore label these movements as smooth tracking to distinguish them from classic smooth pursuit, commonly elicited by the movement of a small, well-defined object (Ilg, 1997). We note, however, that smooth tracking movements elicited by larger patterns have also been labeled as smooth pursuit eye movements (e.g., Heinen & Watamaniuk, 1998), and that the distinction between types of eye movements based on stimulus type alone is generally not possible. In our study, the main distinction is between alternating patterns of saccades as rapid shifts of the eye to a different location in space, and smooth tracking as a slow response that can be either relatively short-lived (and therefore bearing resemblance to optokinetic responses or ocular following) or continuous, pursuit-like.

Eye position data were filtered using a second-order Butterworth filter (low-pass) with a cut-off frequency of 15 Hz. Velocity traces were derived from digitally differentiating the filtered eye positions. Additionally, eye velocities were filtered using a second-order Butterworth filter (low-pass) with a cut-off frequency of 30 Hz. Trials were removed based on visual inspection when a blink occurred before or during stimulus presentation (1.2 % of trials discarded across observers and conditions). We used a velocity-based algorithm to detect saccades (or microsaccades) where eye velocity had to exceed 30°/s (or 5°/s) for a minimum duration of 5 ms. Saccade on– and offsets were then determined as the nearest reversal in the sign of acceleration. The analysis of smooth tracking movements was based on saccade-free position/velocity traces, in which saccades were deleted from each trace. Smooth tracking onset was detected by fitting a piecewise linear function to 2D velocity vectors within 140-ms after stimulus motion onset in each individual trace. We first fitted each 2D position trace with a piecewise linear function, consisting of two linear segments and one breakpoint. The least-squares fitting error was then minimized iteratively (using the function lsqnonlin in MATLAB) to identify the best location of the breakpoint, defined as the time of tracking onset.

To characterize eye movements under different eye movement instructions, we computed and analyzed saccade (and microsaccade) amplitude and peak velocity, and the initial velocity of the smooth tracking response (calculated from tracking onset to first saccade). To evaluate whether eye movements were made to the FOE, we calculated the eye's 2D angular direction error relative to the vector connecting the eye's current 2D position with the FOE position. A saccadic direction error of 0° indicates that the saccade goes to the FOE, whereas a direction error of 180° indicates that the saccade goes away from the FOE. Tracking direction error was computed similarly and then subtracted from 180°. A direction error of 0° indicates tracking in the direction of local dot flow near the fovea, whereas a direction of 180° indicates tracking against the direction of local dot flow. Descriptive measures such as *Median* (*Mdn*) and *Inter-quantile Range* (*IQR*) were used to summarize eye movement measures across observers in each condition. Because each direction error should average to 90° if eye movements went in a random direction (Hooge, Beintema, & van den Berg, 1999), a one-sample Wilcoxon signed-rank test was used to check if direction errors were different from 90° with *d* indicating effect size.

For perceptual performance, we estimated thresholds based on the fitted psychometric functions for each observer using Matlab and Psignifit toolbox version 4.0 (Schütt, Harmeling, Macke, & Wichmann, 2016). A Weibull function (ψ) was fitted to the proportion of correct responses as a function of motion coherence (denoted by *MC*) with the formula below:

$$\Psi(MC;\alpha,\beta,\gamma,\lambda) = \gamma + (1-\gamma-\lambda)F(MC;\alpha,\beta)$$

Specifically, the guessing rate (γ) was fixed at 25 % (chance performance in 4AFC paradigms), whereas the lapse rate (λ, the rate at which observers responded incorrectly regardless of motion coherence) was not fixed as recommended by Wichmann and Hill (2001) but restricted to be under 10 %. Between the lower bound (γ) and the upper bound (λ), the shape of the psychometric function was determined by the threshold (α, motion coherence level at which 75 % performance is reached), and the slope (β, the change in performance at 75 % threshold). The lower the threshold, the lower the motion coherence level an observer can perform the task at, suggesting an overall higher perceptual sensitivity. The steeper the slope, the larger the performance change for a given change in coherence, suggesting a high signal-to-noise ratio or low signal uncertainty (Lu & Dosher, 2008).

2.1.5. Hypotheses and statistical analysis

Two hypotheses evaluated the relationship between different types of naturally occurring or instructed eye movements and optic flow perception. First, we hypothesized that eye movements benefit optic flow direction perception, resulting in better perceptual performance measures (lower threshold, steeper slope) during free viewing vs fixation. We tested differences between eye movement instructions using Wilcoxon signed-rank test, with *d* indicating the effect size. Second, we expected that different levels of perceptual accuracy would be reflected in eye movement metrics. To investigate this, we coded eye movement accuracy based on the direction error (correct eye movement: direction error $< 45°$) and compared perceptual accuracy between trials with correct eye movement direction (resulting in higher accuracy) and incorrect direction (lower accuracy) using a Wilcoxon signed-rank test with *d* indicating the effect size. We also tested whether eye movement metrics were predictive of perceptual judgment accuracy on a trial-by-trial basis using a mixed-effects logistic regression model, for high ($\geq$32 %) and low ($\leq$16 %) motion coherence trials respectively. The alternative model included eye movement metrics as predictors, whereas the null model only included the intercept, to predict perceptual judgment accuracy. Observers were included as a random effect in both models. A chi-square test was used to evaluate whether the alternative model yielded a better fit than the null model, which would indicate that eye movement characteristics predict perceptual judgment accuracy. All statistical analyses were performed using R (R Core Team, 2021), R Studio (Rstudio Team, 2020), and packages *lme4* (Bates, Mächler, Bolker, & Walker, 2015), *effsize* (Torchiano, 2020), and *rstatix* (Kassambra, 2020). The data and the analysis code are available on OSF: https://osf.io/vax7w/?view_only=7a1519a3702342a5bc833b8e46898c13.

2.2. Results

2.2.1. Optic flow perception does not differ between eye movement instructions

Perceptual performance was similar when observers were free to move their eyes compared to when they fixated, both at the individual observer level (Fig. 2**A**) and across observers (Fig. 2**B**).

Whereas both perceptual accuracy and reaction time significantly scaled with motion coherence (accuracy: $F(4,88) = 304.72$, $p <.001$, $\eta^2_G = 8.08$; reaction time: $F(4,88) = 15.30$, $p <.001$, $\eta^2_G = 0.16$), eye movement instruction condition did not interact with motion coherence to affect accuracy ($F(4, 88) = 0.84$, $p =.51$, $\eta^2_G < 0.01$) or reaction time ($F(4, 88) = 0.48$, $p =.75$, $\eta^2_G < 0.01$). Congruently, eye movement instruction condition did not impact discrimination thresholds ($V = 179$, $p =.22$, $d = 0.26$, Fig. 3**A**) and psychometric function slopes ($V = 90$, $p =.15$, $d = 0.30$; Fig. 3**B**), indicating that perceptual performance in our task was comparable regardless of eye movement instruction.

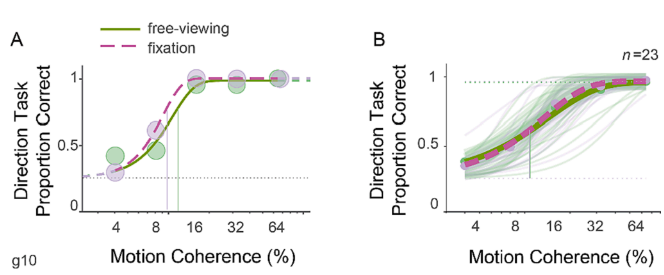

Fig. 2. Perceptual task performance in Exp. 1 of a representative observer (A) indicated by the proportion of trials with correct direction discrimination as a function of motion coherence (colored dots) and the fitted psychometric functions (colored lines), separated by eye movement instruction conditions (green solid: free-viewing vs purple dashed: fixation). The dotted horizontal line indicates chance performance (25%) and the vertical lines indicate the 75% threshold of each condition for this observer. Psychometric functions of individual observers (lighter, thinner lines) and averaged across all observers (darker, thicker lines) are shown in (B).

2.2.2. Eye movement instructions alter the spatial scale of saccades

To characterize eye movements to optic flow, we first examined the spatial characteristics of saccades and analyzed their amplitude and peak velocity across both instruction conditions. Data from a representative observer (Fig. 4**A,B**) and across observers (Fig. 4**C,D)** show that our task produced frequent microsaccades (*Mdn* = 0.2°, *IQR* = 0.1°) in the fixation condition, and larger-amplitude saccades (*Mdn* = 2.4°, *IQR* = 2.1°) in the free-viewing condition. Despite amplitude and peak velocity differences between saccades in the two instruction conditions ($V = 276$, $p <.001$, $d = 0.88$), the relationship between amplitude and peak velocity followed the same linear relationship (main sequence) for both types of saccades (Fig. 4**B**).

Whereas instructions affected the spatial scale of saccades, they did not modulate spatial characteristics of smooth tracking, with comparable amplitude during free-viewing (*Mdn* = 0.34°, *IQR* = 0.2°) and fixation (*Mdn* = 0.25°, IQR = 0.1°; $V = 216$, $p = .02$, $d = 0.50$). These small-scale smooth tracking eye movements had a slow velocity (free-viewing: *Mdn* = 3.4°/s, *IQR* = 1.0°/s; fixation: *Mdn* = 3.3°/s, *IQR* = 1.0°/s; $V = 134$, $p =.92$, $d = 0.03$).

2.2.3. Saccade direction scales with FOE location and smooth tracking direction scales with optic flow direction

Despite spatial scale differences, saccades and microsaccades were similarly directed toward the FOE during free-viewing and fixation, as indicated by relatively small direction errors (Fig. 5**A, C**). As described in the Method section, a saccadic direction error of 0° indicates that the saccade goes to the FOE, whereas a direction error of 180° indicates that the saccade goes away from the FOE. The polar histogram of saccade direction errors reveals similar direction errors for saccades during free-viewing (*Mdn* = 49°) and microsaccades during fixation (*Mdn* = 33°) for one representative observer (Fig. 5**A**). Across observers, the median saccade direction error during free-viewing was 28.2° (*IQR* = 40.7°), not statistically different from the median direction error of microsaccades during fixation (*Mdn* = 44.4°, *IQR* = 39.2°; $V = 74$, $p =.052$, $d = 0.41$, Fig. 5**C**). Saccade direction error of both conditions was significantly different from 90°, the expected average error if saccades were randomly directed (free-viewing: $V = 0$, $p <.001$, $d = 0.86$; fixation: $V = 0$, $p <.001$, $d = 0.86$). These results suggest that the direction of saccadic eye movements is systematically tuned to optic flow regardless of eye movement instruction and spatial scale.

By contrast, smooth tracking eye movements were directed away from the FOE's location. This pattern is revealed by a systematic distribution of tracking direction errors around ~ 0° for one representative

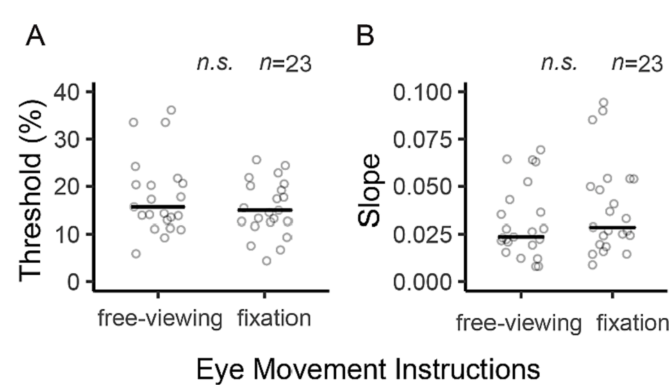

Fig. 3. Threshold (A) and the slope of psychometric function at threshold (B) in Exp. 1 from all observers, as dots with the horizontal position jittered to reduce overlay. Horizontal line indicates group median across observers.

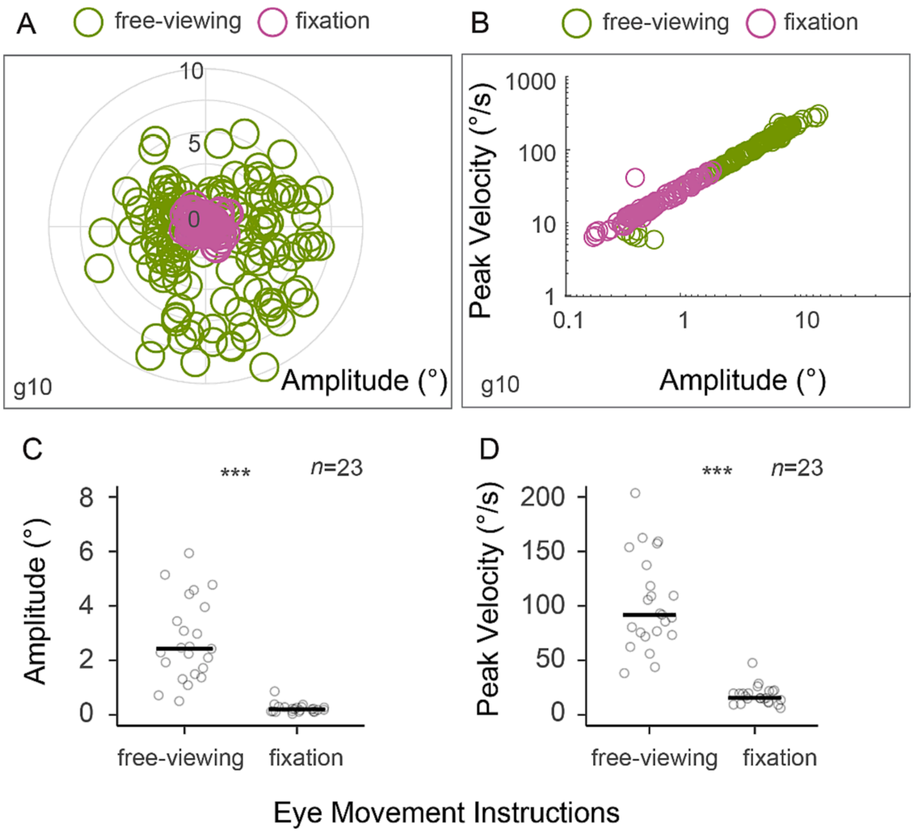

Fig. 4. Spatial characteristics of saccades in a representative observer (A,B) and across observers (C,D) in Exp. 1. In panels A and B, each circle represents a saccade, with line color indicating eye movement instruction condition (green: free-viewing; purple: fixation). In panels C and D, median amplitude and peak velocity from individual observers are represented as dots (horizontally jittered to reduce overlay), whereas the group median across observers is indicated by the horizontal line. Asterisks indicate the *p*-value of paired Wilcoxon tests (***: p <.001).

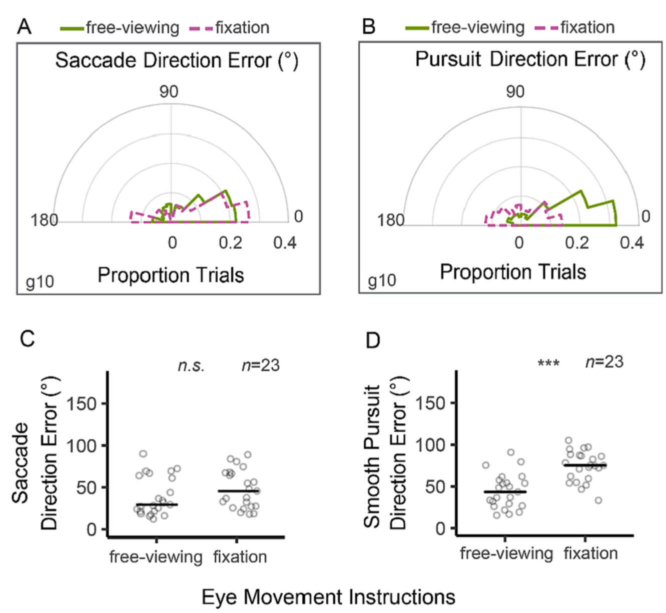

Fig. 5. Directional characteristics of saccades (A,C) and smooth tracking (B,D) in Exp. 1 in a representative observer (A,B) and across observers (C,D), separated by eye movement instruction conditions (green: free-viewing; purple: fixation). In panels C and D, individual observers' median direction errors are represented as dots (horizontally jittered to reduce overlay), whereas the group median across observers (n = 23) is indicated by the horizontal line. Asterisk indicates the *p*-value of paired Wilcoxon test comparing free-viewing and fixation (***: p <.001).

observer (Fig. 5**B**) and across observers (Fig. 5**D**). As described in Methods, a tracking direction error of 0° indicates tracking along the direction of local dot flow near the fovea (and thus away from the FOE). Tracking direction error for both conditions was significantly different from 90° (free-viewing: $V = 1$, p <.001, $d = 0.87$; fixation: $V = 30$, p <.001, $d = 0.69$), suggesting that tracking was not randomly directed. This effect was stronger under free-viewing than under fixation: the median direction error during free-viewing was 43.5° ($IQR = 27.9°$) vs 75.1° under fixation ($IQR = 26.3°$; $V = 18$, p <.001, $d = 0.76$). These findings suggest that the eyes followed the motion direction of the dots that were closest to the fixation location, e.g., if the FOE was located in the upper left quadrant, the lower half of the optic flow stimulus moved in the downward direction, triggering a downward tracking response. In sum, saccades track the FOE location whereas smooth eye movements intuitively track the direction of dot motion near the FOE.

2.2.4. Eye movement direction error can predict perceptual accuracy

We next explored the relationship between perceptual accuracy and eye movement accuracy, i.e., a correct saccade or smooth tracking movement was defined as having a direction error of < 45°. First, we found that perceptual accuracy differed depending on eye movement accuracy. The median perceptual accuracy for correct saccade responses was 88.2 % ($IQR = 13$ %), 36.7 % larger than for incorrect responses ($Mdn = 64.5$ %, $IQR = 14$ %; $V = 248$, p <.001, $d = 0.84$; $F(1,21) = 42.1$, p <.001, $\eta^2_G = 0.26$; Fig. 6A). Parallel to saccade findings, perceptual accuracy was 27.7 % higher for trials in which tracking was in the correct direction (79.5 %, $IQR = 7.5$ %) as compared to those in which an incorrect direction was tracked ($Mdn = 62.3$ %, $IQR = 11.5$ %; $V = 276$, p <.001, $d = 0.88$; $F(1,22) = 47.9$, p <.001, $\eta^2_G = 0.35$; Fig. 6B). Importantly, we found that the relationship between perceptual accuracy and eye movement accuracy was modulated by motion coherence. This observation was confirmed by a significant interaction between saccade accuracy and eye movement instructions when motion coherence was low (coherence ≤ 16 %, $F(1,17) = 4.95$, p =.04, $\eta^2_G = 0.03$), but

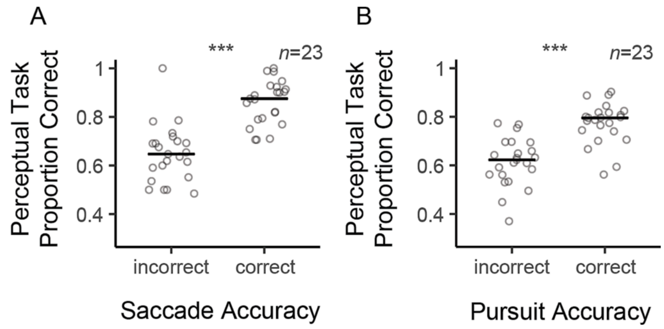

Fig. 6. Perceptual accuracy separated by saccade (A) and tracking (B) direction accuracy in Exp. 1, as dots with the horizontal position jittered to reduce overlay. Horizontal line indicates group median across observers (n = 23). Asterisk indicates the p-value of paired Wilcoxon test (***: p <.001).

not when motion coherence was higher ($F(1,18) = 0.94$, p =.35, η^2_G = 0.01).

To further investigate the link between eye movement accuracy and perceptual accuracy, we examined whether eye movement accuracy could predict perceptual accuracy on a trial-by-trial basis. Eye movement accuracy was found to be a useful predictor of perceptual accuracy only when motion coherence was low (≤16 %), as evident by a significant improvement in model fit when saccade accuracy was included as a predictor ($\chi^2(1) = 21.35$, p <.001). By contrast, including saccade accuracy did not improve model fit when motion coherence was high ($\chi^2(1) = 0.42$, p =.52). Congruently, smooth tracking accuracy as a predictor improved model fit only when motion coherence was low ($\chi^2(1) = 33.17$, p <.001), but not when motion coherence was high ($\chi^2(1) = 0.67$, p =.41). Based on these models, a correct eye movement significantly increased the odds of an observer giving an accurate perceptual response (saccade accuracy: $\beta = 0.62$, $SE = 0.14$, $z = 4.60$, p <.001; tracking accuracy: $\beta = 0.48$, $SE = 0.08$, $z = 5.72$, p <.001) when motion coherence was low. Overall, these results indicate that eye movement directional accuracy is only related to perceptual accuracy when motion coherence is low.

Overall, results from Experiment 1 show that eye movements do not benefit the perception of optic flow in a task where observers locate the FOE coarsely (by reporting the direction of the FOE relative to the screen center). One possible explanation is that our task did not require foveal processing of the FOE, because observers can perform this task by simply attending to the overall direction of dot flow near the screen center, especially at high motion coherence. Hence, eye movements would not necessarily be beneficial. To directly test this assumption, in Experiment 2, we asked observers to report brief visual changes at the FOE. We expected that this task will necessitate foveal processing of the FOE such that eye movements should benefit performance.

3. Experiment 2: Visual change detection at the FOE

3.1. Method

3.1.1. Participants

Eighteen adults (15 female; mean age $M = 22.8$ yrs; $SD = 4.5$ yrs) with normal or corrected-to-normal visual acuity participated in this experiment. All participants provided written informed consent before participation and received CAD 10 per hour of participation as remuneration.

3.1.2. Visual display, stimuli and apparatus

Same as in Exp. 1.

3.1.3. Procedure

During optic-flow stimulus presentation, participants either received no instruction about what to do with their eyes (free-viewing condition), or they were asked to maintain fixation on the fixation cross (fixation condition) as in Exp. 1. Each trial started with a central fixation cross, which remained on screen throughout the trial in the fixation condition, and was removed during free viewing. After the eye tracker performed a drift correction, the optic flow stimulus was presented for 1.5 s. A disc (diameter = 0.3°) was transiently presented twice at the FOE and could either have the same or a different luminance during the second presentation interval.

Specifically, the disc was presented for 8 frames (94 ms) in each presentation, with a brief blank of 8 frames (94 ms) between presentation. The disc could be brighter or dimmer than the background luminance; disc luminance value was adjusted to individual observers such that performance accuracy should be at least 75 % when motion coherence was high under fixation. This value was determined by a titrating block completed after the practice block and before the experimental block. In the titrating block of 50 trials, observers performed the task under fixation with fixed motion coherence (90 %) but varying disc luminance across trials. The disc luminance value of each trial was adjusted with an adaptive QUEST procedure (Watson & Pelli, 1983) to yield a 75 % threshold, which was then used for subsequent test blocks. The average disc luminance value used was 51 % brighter or dimmer against background luminance.

Participants performed a two-alternative forced-choice (2AFC) task to judge whether the briefly presented disc at the FOE reappeared at the same or different luminance (keyboard press "j" for same luminance, "f" for different luminance; Fig. 7). After judgment, the central fixation cross turned green to indicate a correct response, and red to indicate an error (Fig. 7).

Participants completed 56 trials for each of the five motion coherence levels (4 %, 8.7 %, 19 %, 41 %, or 90 %), yielding a total of 280 trials per eye movement condition. Motion coherence was randomized within each block of trials, and eye movement instructions were blocked; the order of eye movement instruction was counterbalanced across participants. Prior to the experiment, participants completed practice trials of 30 trials for each eye movement instruction, and a titrating block of 50 trials, during which the disc luminance difference between first appearance and reappearance are adaptively adjusted to reach a 75 % accuracy in change detection judgement when fixating. Including practice blocks, a titrating block to determine disc luminance value for each observer, and breaks between blocks, the experiment took about 120 min to complete.

3.1.4. Eye movement data preprocessing and analysis

In addition to the same preprocessing and analysis done in Exp. 1, we also extracted d prime (d') as an indicator of performance, due to the change detection nature of the task. d' was computed based on hit rate (observers reporting a change of luminance when there was a change) and false alarm rate (observers reporting a change of luminance when there was not a change) with the formula below:

$$d' = z(hitrate) - z(falsealarmrate)$$

3.1.5. Hypotheses and statistical analysis

We hypothesized that eye movements will benefit perception in this task, which requires foveal processing. Specifically, eye movements should benefit visual perception at the FOE, resulting in better luminance change detection performance (higher d') during free viewing vs fixation. To test for this effect, we conducted a repeated measures ANOVA with two factors, eye movement instruction and motion coherence, with η^2_G indicating the effect size. Second, we expected that eye movement metrics are related to accuracy in perceptual judgment. To investigate this relationship as in Exp. 1, we compared perceptual accuracy between trials with correct eye movement direction (resulting in higher accuracy) and incorrect direction (lower accuracy) using a Wilcoxon signed-rank test with d indicating the effect size, and explored

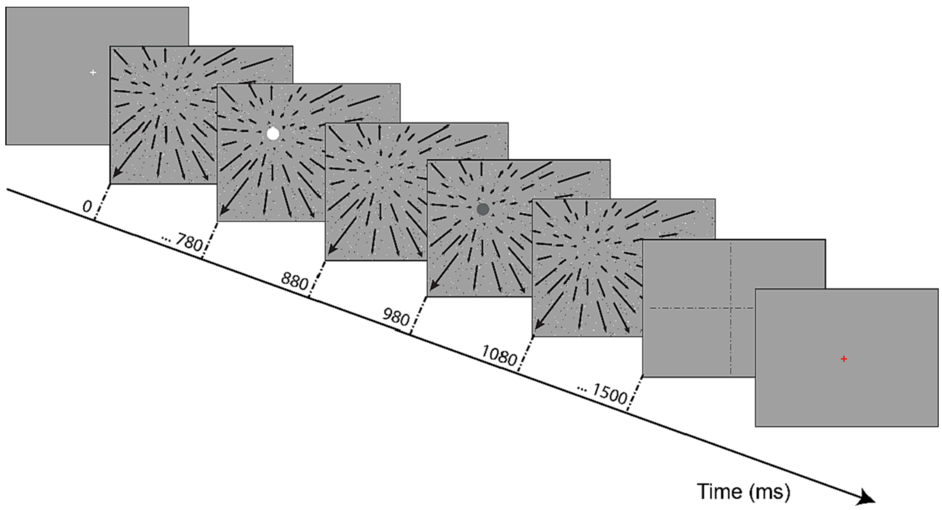

Fig. 7. Trial timeline in Exp. 2 with approximate event onset indicated by time from trial onset (ms). For illustrative purpose, arrows are plotted to indicate the local dot direction of optic flow (arrows not shown during experiment), and disc size is enlarged.

whether eye movement metrics were predictive of perceptual judgment accuracy on a trial-by-trial basis using mixed-effects logistic regression modelling. All statistical analyses were performed using R (R Core Team, 2021), R Studio (RStudio Team, 2020), and packages *lme4* (Bates, Mächler, Bolker, & Walker, 2015), *effsize* (Torchiano, 2020), and *rstatix* (Kassambra, 2020).

3.2. Results

3.2.1. Perceptual performance at the FOE is better under free-viewing vs Fixation

Observers were highly accurate in detecting brief visual changes, yielding a median perceptual sensitivity of $d' = 2.70$ ($IQR = 0.89$). In some observers, d' increased with motion coherence levels, whereas in others, d' remained stable regardless of motion coherence levels. Overall, d' was higher during free-viewing ($Mdn = 2.91$, $IQR = 0.31$) vs fixation ($Mdn = 2.30$, $IQR = 0.36$), confirmed by a significant main effect of eye movement instructions ($F(1,17) = 19.4$, $p < .001$, $\eta^2_G = 0.08$; Fig. 8**A,B**). Furthermore, the effect of eye movement instructions interacted with motion coherence ($F(4,68) = 7.77$, $p < .001$, $\eta^2_G = 0.04$). To understand this interaction effect, we examined the effect of eye movement instructions when motion coherence was low vs high, respectively. When motion coherence was low ($\leq$20 %), change detection sensitivity under free-viewing was 22.4 % higher ($Mdn = 2.83$, $IQR = 0.31$) than during fixation ($Mdn = 2.31$, $IQR = 0.34$, $V = 465$, $p = .04$, $d = 0.35$, Fig. 8**A**). The effect of eye movement instruction was more apparent when motion coherence was high, where change detection sensitivity under free-viewing was 45.3 % larger ($Mdn = 3.40$, $IQR = 0.29$) than during fixation ($Mdn = 2.34$, $IQR = 0.38$, $V = 666$, $p < .001$, $d = 0.87$, Fig. 8**B**).

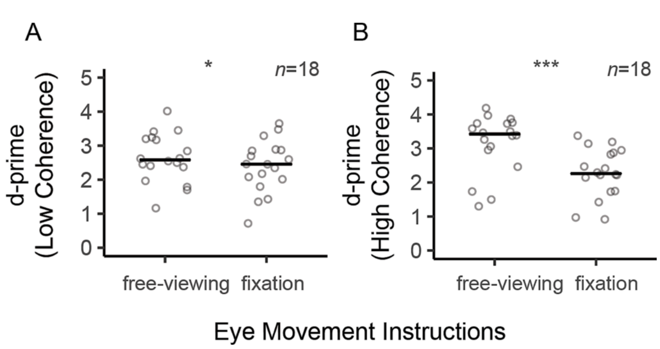

Fig. 8. d-prime measures for low (A) and high (B) motion coherence levels in Exp. 2, as dots with the horizontal position jittered to reduce overlay. Horizontal line indicates group median across observers ($n = 18$). Asterisk indicates the p-value of paired Wilcoxon test (*: $p < .05$, ***: $p < .001$).

Overall, detection sensitivity at the FOE might have benefitted from free-viewing eye movements, more strongly so when motion coherence is high. To be able to detect visual changes at the FOE, observers need to first locate the FOE, which is more difficult when motion coherence is low, limiting potential benefits of eye movements. Results in experiment 2 suggest that observers use FOE location—afforded by high motion coherence—as a cue for luminance change detection.

3.2.2. Saccade but not tracking direction error predicts perceptual accuracy

Similar to Exp. 1, we explored the link between perceptual task accuracy and eye movement accuracy. Before doing so, we needed to first establish that eye movements in this experiment showed similar characteristics as in those in Exp. 1, which was the case. For example, eye movements occurred regardless of eye movement instructions, with eye movement instructions affecting the spatial scale of saccades (larger amplitude under free-viewing vs fixation, $V = 153$, $p < .001$, $d = 0.88$) but not tracking (similar velocity under free-viewing and fixation, $V = 76$, $p = 1$, $d < 0.01$). Another example would be that saccades were directed towards the FOE, and smooth tracking followed the retinal motion, as indicated by small direction errors (saccade: $Mdn = 25.2°$, $IQR = 23.4°$; tracking: $Mdn = 45.2°$, $IQR = 22.5°$) when motion coherence was high, which were different from 90° (saccades under free-viewing: $V = 0$, $p < .001$, $d = 0.88$; saccades under fixation: $V = 14$, $p = .002$, $d = 0.72$; tracking under free-viewing: $V = 0$, $p < .001$, $d = 0.88$; tracking under fixation: $V = 1$, $p < .001$, $d = 0.87$). Given the strong effect of eye movements on perceptual performance, it can be expected that eye movements directed successfully toward the FOE would improve observers' task performance.

Perceptual task accuracy was higher when saccades were correct ($Mdn = 91.6$ %, $IQR = 5.7$ %) vs incorrect ($Mdn = 89.3$ %, $IQR = 9.8$ %; $V = 120$, $p = .04$, $d = 0.50$). This link between saccade accuracy and perceptual accuracy depended on motion coherence, as further investigated by a trial-by-trial mixed logistic regression modelling as follows. When motion coherence was low (coherence $\leq$ 20 %), including saccade accuracy as a predictor improved model fit compared to the null model ($\chi^2(1) = 4.23$, $p = .04$), such that an accurate saccade increased the odds of making an accurate perceptual judgement ($\beta = 0.24$, $z = 2.05$, $p = .04$). When motion coherence was high (coherence greater than 40 %), saccade accuracy did not improve model fitting ($\chi^2(1) = 2.96$, $p = .09$). Contrary to saccade results, perceptual accuracy did not differ based on tracking direction accuracy ($V = 87$, $p = .64$, $d = 0.12$). This null result is reflected by our modelling result: including tracking accuracy did not improve model fit compared to null model when motion coherence was low ($\chi^2(1) = 0.02$, $p = .90$) or high ($\chi^2(1) = 0.16$, $p = .69$).

Given the relation between saccade direction accuracy and perceptual accuracy we next analyzed saccade endpoint error to understand whether the observed performance benefit might be due to the simple fact that a saccade brings the fovea closer to the FOE, thereby improving task performance. If that were the case, we would expect that higher saccade endpoint error (defined as the Euclidean distance between saccade endpoint and FOE location) should be related to lower perceptual accuracy, and saccade endpoint error should be a significant predictor in the trial-by-trial analysis. Our analysis confirmed this expectation. Including saccade endpoint error as a predictor improved model fitting for low motion coherence ($\chi^2(1) = 6.56$, $p = .01$), such that an increase in saccade endpoint error decreased perceptual judgment accuracy ($\beta = -0.06$, $z = -2.67$, $p = .008$). Interestingly, including saccade endpoint error also improved model fitting when motion coherence was high (relative to the null model: $\chi^2(1) = 15.15$, $p < .001$). Similar to the effect observed when motion coherence was low, an increase in saccade endpoint error was associated with a decrease in perceptual accuracy when motion coherence was high ($\beta = -0.12$, $z = -3.62$, $p < .001$).

In sum, observers are better able to detect visual changes at the FOE when saccades are directed to the FOE as compared to when saccades are not directed to the FOE. This result further supports the idea that eye movements benefit perception in this task. We did not find a relationship between tracking direction accuracy and perceptual accuracy, presumably because directing tracking along the retinal motion direction actually directs attention away from the FOE, cancelling out performance benefits of eye movements.

4. General discussion

In this study, we show that optic flow patterns trigger saccade and tracking eye movements even in the absence of an instruction to move the eyes. The characteristics of the resultant large-scale (free viewing) and small-scale (fixation) eye movements fall along a continuum, congruent with what has been reported for microsaccades (Otero-Millan, Macknik, Langston, & Martinez-Conde, 2013; Zuber, Stark, & Cook, 1965). These results emphasize the usefulness of optic flow patterns as stimulation material for eye movements. Notwithstanding the rich pattern of intuitive eye movement responses, eye movements do not always enhance optic flow perception. Only under difficult stimulus conditions (for example, low motion coherence), or specific task conditions (for example, detecting brief visual changes at the FOE) do eye movements benefit perceptual performance. The task-dependency of the benefits of eye movements mirrors the functions of eye movements in visual perception. Eye movements serve to provide useful information to the perceptual system only in situations and tasks in which they are necessary because the task requires foveal vision.

4.1. Eye movement characteristics during optic flow perception

Saccades and tracking eye movements intuitively follow the FOE and dot motion, in replication of our previous findings (Chow et al., 2021). The current study extends these findings to microsaccades and shows that they behave similarly to saccades and are directed at the FOE (vs away from the FOE as in Piras et al., 2016). This directional tuning of saccades and microsaccades toward the FOE could imply a natural orienting response to the heading direction (Higuchi, Inoue, Endo, & Kumada, 2019; 2020; Wang, Fukuchi, Koch, & Tsuchiya, 2012). Such overt (saccades) and covert (microsaccades) orienting might be especially useful in actively monitoring heading direction in tasks involving visual guidance of actions, such as walking and steering. Following this logic, rapid orienting of saccades to the FOE could facilitate the detection and identification of a visual target that serves as the destination (or presents a distractor or obstacle), and the calibration of heading direction relative to the destination or obstacle. Indeed, the importance of eye movements in tasks such as walking has been amply demonstrated in studies examining the relation between gaze and foot placement during multi-terrain walking (Matthis et al., 2018) or obstacle crossing (Hayhoe, Gillam, Chajka, & Vecellio, 2009; Bonnen et al., 2021).

Whereas saccades are directed at the FOE, slow and smooth eye movements to optic flow follow the retinal motion of dot flow near the fovea. Smooth tracking is tuned to the retinal motion direction and motion signal strength, in alignment with previous work indicating that human (Niemann, Lappe, Büscher & Hoffmann, 1999) and non-human primate observers (Lappe, Pekel & Hoffmann, 1998) show slow-phase tracking of foveal motion in response to a large field of optic flow stimulus under free-viewing.

The slow speed ($<3^\circ/s$) of the smooth tracking response observed in our study resembles the characteristics of micro-pursuit (e.g., Parisot, Zozor, Guérin-Dugué, Phlypo, & Chauvin, 2021), or ocular position drift during fixation (e.g., Malevich, Buonocore, & Hafed, 2020), albeit with a higher speed than previously reported (Schneider, Thurtell, Eisele, Lincoff, Bala, & Leigh, 2013). Whereas these eye movements are typically triggered by static stimuli (e.g., Necker cube used in Parisot et al., 2021, and low-spatial-frequency Gabor patterns used in Malevich et al., 2020), our work shows that these drifting eye movements can arise naturally in response to optic flow.

In sum, optic flow can be a powerful stimulus to elicit a multitude of naturally-occurring eye movements (saccades, smooth tracking, fixational eye movements). The tuning of eye movements to stimulus properties (e.g., FOE location for saccades and retinal motion for tracking) is preserved across spatial scales and tasks. Future work can address the potential interaction between different kinds of eye movements (e.g., saccades and smooth tracking or smooth pursuit) as well as improve our understanding of the circumstances from which they arise.

4.2. Role of eye movements during the perception of optic flow direction

Eye movements serve many functions such as bringing the object of interest to the fovea, reducing motion blur, and providing extra-retinal cues to target motion (Leigh & Zee, 2015). Whereas the importance of eye movements for visual motion perception has been established in tasks such as motion prediction (Bennett, Baures, Hecht, & Benguigui, 2010; Spering, Schütz, Braun & Gegenfurtner, 2011) and motion extrapolation (Becker & Fuchs, 1985; Barnes, 2008), we show that executing an eye movement does not always benefit the perception of optic flow direction. Rather, the benefits of eye movements for optic flow perception are specific to the demands of the task. Sometimes, the task-dependent benefits of eye movements also depend on stimulus properties.

The benefit of eye movements on optic flow perception is more likely to be observed when foveal processing of optic flow stimulus is required. In Exp. 2, where we observed a benefit of eye movements, observers likely needed to foveate the FOE to detect brief changes to the visual stimulus. In support of this assumption we observed a link between saccade endpoint error and perceptual accuracy: a smaller distance between saccade endpoints relative to the FOE was associated with higher perceptual accuracy. The performance benefit of the free-viewing instruction in this task reflects previous research findings showing better visual performance at the FOE location (Wang et al., 2012; Higuchi et al., 2019). It will be important to further investigate the influence of eye movements in a variety of tasks related to optic flow perception. For example, saccades are likely going to benefit other perceptual tasks that require higher visual acuity, such as when observers are asked to monitor small FOE location changes. Smooth tracking (or pursuit in general) is likely going to benefit optic flow perceptual tasks that require direction or speed judgments. Moreover, it is possible that task difficulty played a role in our study, and that eye movements might facilitate performance more in situations in which visual information is sparse (low stimulus contrast, low motion coherence, short presentation duration, etc.). Congruent with this assumption, we found correlations between the accuracy of saccade direction and perceptual performance in both tasks, but only when motion coherence was low. In a previous study, we showed that smooth pursuit eye movements enhance the perception of motion direction when a stimulus is shown for a brief period of time (Spering et al., 2011), emphasizing the importance of eye movements in difficult perceptual tasks and under visual uncertainty (Fooken, Kreyenmeier, & Spering, 2021).

Notwithstanding the clearer influence of macro eye movements on optic flow perception in select tasks, the functional role of fixational eye movements on optic flow perception remains to be explored. It is unclear what kind of micro retinal inputs could benefit heading judgments—a task that usually requires large-scale tracking eye movements and leads to large position shifts. It is well known that fixational eye movements benefit performance at the locus of attention (Hafed & Clark, 2002; Laubrock, Engbert, & Kliegl, 2005; Liu, Nobre, & van Ede, 2022; Yu, Herman, Katz, & Krauzlis, 2022), and that microsaccade occurrence and direction are tuned to informative regions of scenes and faces (McCamy, Otero-Millan, Di Stasi, MacKnik, & Martinez-Conde, 2014; Shelchkova, Tang, & Poletti, 2019). Congruent with this finding is our observation that microsaccade direction is tuned to the FOE, the most informative region of the stimulus used across experiments. One possibility is that fixational eye movements close to the FOE might serve to produce unique retinal inputs benefitting fine-grained visual tasks such as improving visual acuity (Intoy & Rucci, 2020) or feature discrimination at the FOE. However, the exact impact of micro eye movements on perception at the FOE is unclear.

4.3. Potential utility of eye movements as indicators of optic flow sensitivity

Given the rising interest in using eye movements as a window to perception, we discuss the potential utility of eye movements in indicating perceptual sensitivity to optic flow. First, eye movements are more responsive to the FOE as motion coherence increases. This sensitivity to stimulus factors is consistent with previous demonstrations that ocular tracking of heading changes is sensitive to motion coherence (Chow et al., 2021) and other stimulus properties (contrast: Chow et al., 2021; speed: Chow et al., 2021, Cornelissen & van den Dobbelsteen, 1999; size of stimulus field: Cornelissen & van den Dobbelsteen, 1999; flow direction: Shirai & Imura, 2016). Second, saccadic direction error is larger in trials when perceptual judgment is incorrect (Exp. 1, 2), supporting the potential link between eye movement measures and perception, similar to previously reported relationship between reflexive (Dakin & Turnbull, 2016; Essig, Sauer, & Wahl, 2021) or voluntary (Mooney, Hill, Tuzun, Alam, Carmel, & Prusky, 2018; Mooney, Alam, Hill, & Prusky, 2020) eye movements and perception.

Our study also revealed some limitations of using eye movements to indicate perceptual performance properties. For instance, eye movements to optic flow did not occur every trial under free-viewing, unlike other paradigms where eye movements are always elicited (e.g., when observers are explicitly instructed to track a moving dot). The occurrence of these eye movements also varied between observers, where some observers were more inclined to make these eye movements, and others less so. Using such measures to indicate perceptual accuracy requires careful design of task instructions.

5. Conclusion

The tight link between optic flow and eye movements serves many functions from stabilizing gaze to allowing one to quickly change course in response to danger. We found that eye movements affect optic flow perception under specific stimulus and task conditions. Moreover, naturally-occurring eye movements in response to optic flow show characteristics corresponding to stimulus difficulty and perceptual accuracy. Eye movements during optic flow might therefore be both influential and consequential to perception, serving a dual purpose in affecting and revealing optic flow perception.

CRediT authorship contribution statement

Hiu Mei Chow: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Miriam Spering:** Conceptualization, Data curation, Funding acquisition, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

I have shared the link to my data/code in the manuscript.

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