Dissociation between perception and smooth pursuit eye movements in speed judgments of moving Gabor targets

Anna E. Hughes

Centre for Life and Environmental Sciences, University of Exeter, Penryn, UK
Department of Physiology, Development & Neuroscience, University of Cambridge, Cambridge, UK

The relationship between eye movements and subjective perception is still relatively poorly understood. In this study, participants tracked the movement of a Gabor patch and made perceptual judgments of its speed using a two-interval forced choice task. The Gabor patch could either have a static carrier or a carrier moving in the same or opposite direction as the overall envelope motion. We found that smooth pursuit speed was strongly affected by the internal motion of the Gabor carrier, with faster smooth pursuit being made to targets with internal motion in the same direction as overall motion compared to targets with internal motion in the opposite direction. However, we found that there were only small and highly variable differences in the perceptual speed judgments made simultaneously, and that these perceptual and smooth pursuit measures did not significantly correlate with each other. This contrasts with the number of catch-up saccades (saccades made in the direction of overall target motion), which was significantly correlated with the simultaneous perceptual judgments. There was also a significant correlation between perceptual judgments and the difference between the target and eye position immediately before a saccade. These results suggest that it is possible to see dissociations between vision and action in this task, and that the specific type of visual action studied may determine the relationship with perception.

Introduction

A key unresolved question in the study of eye movements is to what extent they can be considered independent of perceptual experience. Several recent reviews have summarized our knowledge of the relationship between smooth pursuit eye movements and perception (Schütz, Braun, & Gegenfurtner, 2011; Spering & Montagnini, 2011). In some cases, it has been shown that visual perception of a moving target and pursuit eye movements are strongly linked. Direction biases seen in perception (such as the oblique effect) can also be seen in smooth pursuit trajectories (Krukowski & Stone, 2005). In addition, direction discrimination thresholds for smooth pursuit and perception have been shown to be similar and also show high trial-by-trial covariation (Mukherjee, Battifarano, Simoncini, & Osborne, 2015; Stone & Krauzlis, 2003). Recent work has also shown that smooth pursuit eye movements and perception show similar illusory shifts in direction perception when tracking a stimulus with both internal and envelope motion (Lisi & Cavanagh, 2015). These results have therefore been used to argue that smooth pursuit eye movements and direction perception share some neural mechanisms and are not processed entirely separately.

For speed perception, however, the data are more mixed. There are qualitative similarities between smooth pursuit and speed perception: For example, smooth pursuit acceleration (at the beginning of a trial) is reduced for isoluminant color stimuli (Braun et al., 2008), and it has been shown in many studies that isoluminant color stimuli are perceived to be moving more slowly than luminance stimuli of matched contrast during fixation (Braun et al., 2008; Cavanagh, Tyler, & Favreau, 1984; Gegenfurtner & Hawken, 1996a; Gegenfurtner & Hawken, 1996b). Similarly, reduced contrast luminance stimuli are both perceived as moving more slowly (Thompson, 1982) and are pursued more slowly (Spering, Kerzel, Braun, Hawken, & Gegenfurtner, 2005). Finally, a number of studies have found good matches between speed discrimination thresholds for perception and pursuit (Gegenfurtner, Xing, Scott, & Hawken, 2003; Kowler & McKee, 1987; Mukherjee et al., 2015).

However, there have also been findings that suggest a dissociation between speed perception and pursuit. Several studies have found that, when tracking, participants perceive the speed of chromatic stimuli accurately, contrasting with studies that have found

Citation: Hughes, A. E. (2018). Dissociation between perception and smooth pursuit eye movements in speed judgments of moving Gabor targets. *Journal of Vision*, *18*(4):4, 1–19, https://doi.org/10.1167/18.4.4.

https://doi.org/10.1167/18.4.4 Received September 15, 2017; published April 3, 2018 ISSN 1534-7362

reductions in the speed of smooth pursuit (Braun et al., 2008; Cavanagh et al., 1984; Terao & Murakami, 2011). Pursuit has been shown to be more accurate than perception in an experiment involving detecting a velocity perturbation within a moving target (Tavassoli & Ringach, 2010), and there appears to be no trial-by-trial covariation between speed perception and pursuit (Braun, Pracejus, & Gegenfurtner, 2006; Gegenfurtner et al., 2003). The differences seen between speed and direction when considering the relationship between pursuit and perception are probably due in part to the more complex calculations required for speed perception. The direction tuning of individual MT neurons can be directly related to the direction of pursuit; however, MT neurons respond to a range of speeds, and therefore speed has to be calculated from the population response (Schütz et al., 2011).

Many studies have used relatively simple experimental paradigms, where a small pursuit target moves across a uniform background. However, there is increasing interest in studying more complex tasks. In one experiment (Spering & Gegenfurtner, 2007) participants were asked to pursue a target and judge its speed when either the target speed or the speed of a peripheral grating surrounding the path of the target could be perturbed. In this case, pursuit and perception were found to be very different, with pursuit showing an integration of the target and context speed, but perception showing a contrast between the two speeds.

Speed judgments can also be made more complex by incorporating both carrier and envelope motion within the target. It is well known that speed and direction perception can be affected by the internal motion of a moving target whilst a participant is fixating at a specific point (Hisakata, Terao, & Murakami, 2013; Hughes, Fawcett, & Tolhurst, 2015; Lisi & Cavanagh, 2015; Shapiro, Lu, Huang, Knight, & Ennis, 2010; Zhang, Yeh, & De Valois, 1993). One recent study has shown quantitatively that speed judgments can also be biased in a similar manner while tracking the target (Hall et al., 2016). Furthermore, it is known that steady state smooth pursuit to this type of second order stimulus is less precisely matched to the velocity of the target, particularly for relatively slow motion (1°/s), and the resulting errors are corrected by saccades (Butzer, Ilg, & Zanker, 1997; Hawken & Gegenfurtner, 2001). However, perceptual judgments and smooth pursuit eye movements have not previously been studied in the same task, and therefore it is of interest to investigate whether the biases in speed perception map onto smooth pursuit errors in a systematic manner.

Therefore, in this study, we have further investigated the speed perception of Gabor stimuli that contained either a static carrier or a carrier moving in the same or the opposite direction as the overall envelope motion. We first conducted a preliminary experiment where participants made speed perception judgments in a two-interval forced choice task. We predicted that subjects would show speed biases in line with previous results (Hisakata et al., 2013; Lisi & Cavanagh, 2015; Shapiro et al., 2010; Zhang et al., 1993), with perceived speed being slower for carrier motion in the opposite direction to overall envelope motion and faster for carrier motion in the same direction. We then carried out the main experiment, where participants tracked the moving stimulus and were again asked to make a perceptual speed judgment. During the trial, we also measured the speed of the smooth pursuit made to the target. We asked whether the speed of smooth pursuit and the perceptual judgments showed similarities overall and also analyzed whether perception and smooth pursuit showed a correlation on a trial-by-trial basis. We predicted, based on previous results (Braun et al., 2006; Gegenfurtner et al., 2003; Kowler & McKee, 1987; Mukherjee et al., 2015; Tavassoli & Ringach, 2010), that there would be an overall correlation but not a trial-by-trial correlation between smooth pursuit speed and perceptual judgments on this task.

To preview the results, we found that when participants tracked the targets there were strong and consistent differences in smooth pursuit speed between different drift types, but that these differences were smaller and more variable in the case of the simultaneous perceptual judgments. This contrasts with the preliminary data, which showed strong perceptual biases when the participants were fixating, and these biases were qualitatively similar to those seen in smooth pursuit speed. We extended previous work by also considering whether saccadic eye movements differed between the different drift types, and whether this could help us to understand the differences between perception and smooth pursuit in this task. We found that there were significantly different numbers of catch-up (in the direction of target motion) and step-back (opposite to target motion) saccades in the different conditions, and that perceptual judgments significantly correlated with the number of catch-up saccades. We also found that the error in eye position compared to target position differed between different conditions, and that there was a significant correlation between the error immediately prior to a saccade and the perceptual judgments.

Methods

General methods

Stimuli were presented on a 19-in. SONY CRT display at a frame rate of 120 Hz by a ViSaGe system (Cambridge Research Systems Ltd., UK) that was programmed using the CRS toolbox for MATLAB

(MathWorks, Natick, MA). The screen resolution was 800 × 600 pixels, and from the viewing distance of 57 cm, the screen subtended 38.2° × 28.7°. The background of the display was a uniform midgray (60 cd/m^2).

The stimuli used in these experiments were vertically oriented Gabor patches with a spatial frequency of 3 cycles/deg (standard deviation: 0.5°; visual extent: 1.9°) and a Michelson contrast of 1.0. The standard stimulus always moved at 8°/s and had no internal motion of the carrier. The comparison stimulus could have no movement of the carrier stripes (no-drift condition) or could have internal motion, either at 6 Hz in the same direction as the overall direction of travel (forwards-drift condition) or at 6 Hz against the direction of travel (backwards-drift condition). These two drift types could be presented in either order (i.e., standard first or comparison first). The participant's task was always to indicate which of the two stimuli they thought had moved faster by pressing a button on the keyboard to indicate their choice.

In total, 19 participants took part in the two experiments. There were four participants (one male) in the preliminary experiment and 15 (four male) in the main experiment (there was no overlap in observers between the two experiments). All observers gave written consent to take part. The research was carried out in accordance with the Declaration of Helsinki and was approved by the Psychology Research Ethics Committee at the University of Cambridge.

Preliminary experiment

Two of the participants in this experiment (Participants 1 and 2) were experimenters who were experienced psychophysical observers and two were naïve participants (Participants 3 and 4). Participants were instructed to fixate a spot in the center of the target trajectory; this spot was present for the whole duration of the trial.

On each trial, targets moved from left to right laterally across the screen, always passing through the vertical midline. The exact distance the patch traveled was randomized on each presentation to ensure that time on screen could not be used as a cue to the speed of the target, and could be anywhere between 14.25° and 23.75° long in total. Each comparison stimulus type was presented in two staircases, with the initial starting speeds of the staircases being 13.5°/s and 3.5°/s (i.e., one staircase started at a faster speed than the standard stimulus and one staircase started at a slower speed than the standard stimulus). If a participant correctly judged which of the standard and comparison was moving faster on two consecutive trials, the difference in speeds between standard and comparison was decreased (making the judgment harder). However, if the participant made one mistake, the difference in speeds between standard and comparison was increased (making the judgment easier). The program was designed such that the standard and comparison could never be equal in speed and thus there was always a correct option. Presentation of the six different staircases was interleaved, and each staircase ended after 16 reversals (changes in direction of the staircase). Each participant completed four repeats of the full experiment, giving approximately 1,000 trials for each participant.

Main experiment

On each trial, a fixation square was presented on one side of the display (Figure 1, top panel), at an X position of 500 pixels (offset to the right of the screen, approximately 15° from the right hand edge) and a Y position of 0 pixels (in the center of the screen). This square was presented for 500 ms and the participant was instructed to fixate it. The square then disappeared and a vertically oriented Gabor appeared at the same location. It then moved across the screen from right to left for a fixed distance of 200 pixels (approximately 10°) and participants followed this movement with their eyes (Figure 1, second panel). After a short break of 200 ms (Figure 1, third panel), the fixation square was then presented again for 500 ms (Figure 1, fourth panel), which the participant fixated until tracking a second target that moved across the screen for the same distance as the first (Figure 1, fifth panel). In this experiment, the comparison stimulus moved at one of 10 different speeds: 5°/s, 6°/s, 6.5°/s, 7°/s, 7.5°/s, 8.5°/s, 9°/s, 9.5°/s, 10°/s, or 11°/s.

In each block, each type of comparison target was presented at each speed twice in a random order, giving a total of 60 trials in each block (i.e., three internal drift conditions, at 10 speeds, twice). All 15 volunteers that took part in the experiment were naive to the experimental aims. Each participant completed 10 blocks in total, giving 600 trials in the complete experiment, and each block was always preceded by eye tracking calibration and validation. Participants were also given a brief training period at the beginning of the experiment where they completed 10 trials in order to become familiar with the procedure.

Participants were seated with their head stabilized by a chin rest and forehead support, in a dimly lit room. They viewed the stimulus binocularly and eye movements of their left eye were recorded at 1000 Hz using a desktop mounted Eyelink eyetracker that uses an infrared camera to record the movements of the pupil and iris (Eyelink 1000; SR Research Ltd, Mississauga, Ontario, Canada). Calibration and validation used standard procedures from the Eyelink toolbox in Psychtoolbox (Brainard, 1997; Pelli, 1997).

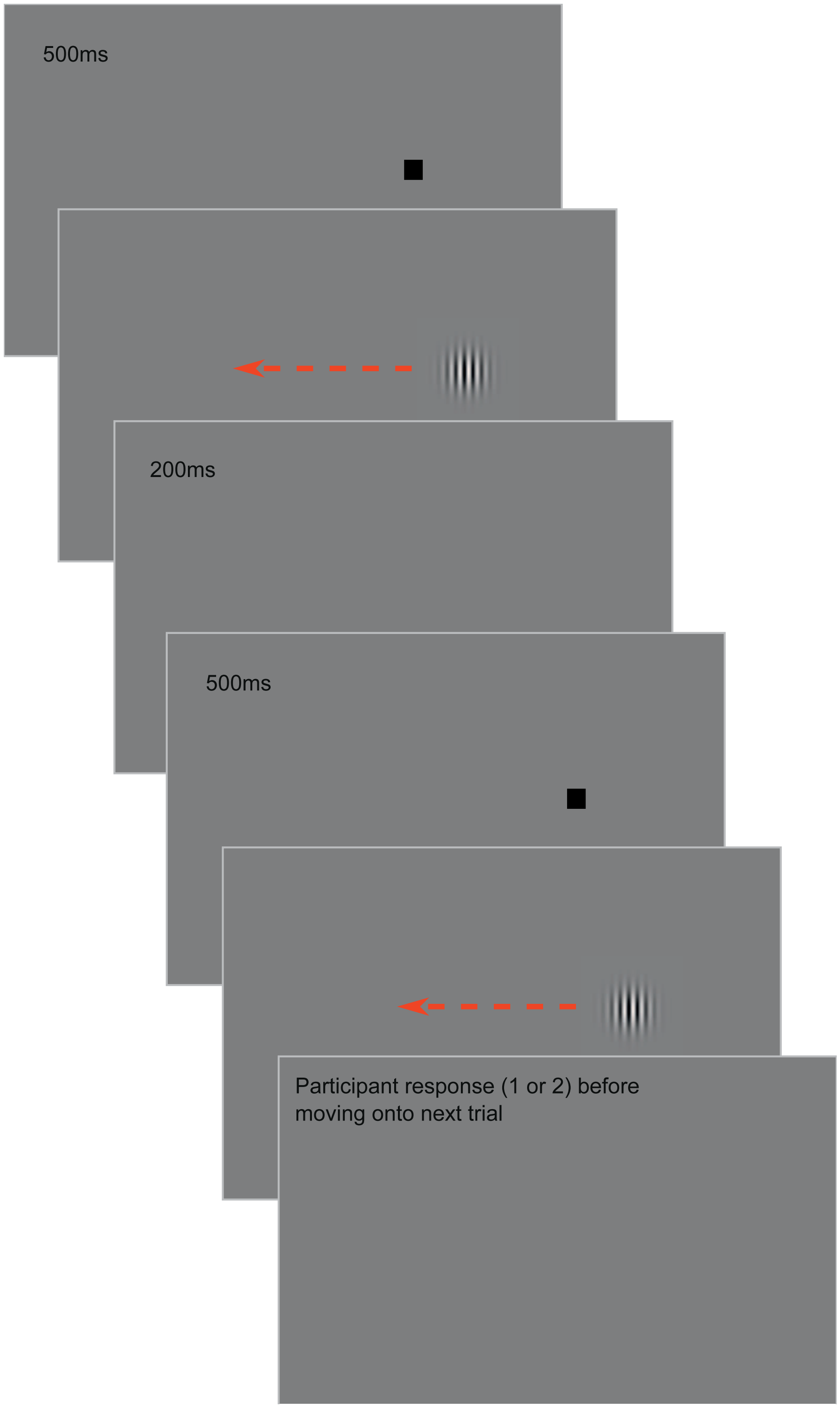

Figure 1. Diagram to show the general set up of the experiment. On each trial, participants viewed two moving targets (as pictured) and used the keyboard to indicate which they thought had moved faster. Presentation could either be comparison first, standard second or standard first, comparison second. (Image not to scale.)

Perceptual analysis

For both the preliminary and main experiment, points of subjective equality (PSE) for each participant (i.e., the true speed at which the comparison stimulus was perceived as moving faster than the standard 50% of the time) were estimated using the *quickpsy* package (version 0.1.4; Linares & Lopez-Moliner, 2016) in R (version 3.4.1; Ihaka & Gentleman, 1996). Graphs were plotted using the ggplot2 package (version 2.2.1; Wickham, 2009).

For hypothesis testing we used generalized linear mixed models (GLMM) to fit psychometric functions to the data, with a binomial logistic error structure being used to account for the fact that the response variable was binomial (the comparison was either perceived as moving faster or slower than the standard). These were fitted using the *lme4* package (version 1.1-14; Bates, Mächler, Bolker, & Walker, 2014) and the *lmerTest* package (version 2.0-33; Kuznetsova, Brockhoff, & Christensen, 2014). Participant ID number was included in the models as a random factor, allowing the model to account for variance across participants, while still allowing determination of whether the dependent variable (proportion correct) depended on the comparison target drift type presented across all participants tested.

For both experiments, a full model was initially fitted on all trials using all fixed factors of interest (comparison speed and drift type) and their interactions. The model was then simplified based on the Akaike information criterion and log likelihood to produce a best-fit model (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The best random effects structure for the preliminary experiment had comparison speed as a random slope for the participant number random intercept. The best random effects structure for the main experiment included drift type and comparison speed as random slopes for the participant number random intercept.

Smooth pursuit analysis

Recorded eye movement traces were stored on disk and analyzed offline using MATLAB (MathWorks) via import using the *edfImport* library (Pastukhov, 2011). A small number of trials (10 in total) had to be removed from further analysis due to nonsystematic technical errors. Analysis of the eye movement recordings was carried out using customized MATLAB scripts, as smooth pursuit is not identified by the Eyelink parser. The following analysis was carried out for both standard and comparison targets separately for each trial.

The analysis began from 300 ms after the initial presentation of the stimulus (as this was approximately the time taken across participants for the smooth pursuit to ramp up to a steady state). Any part of the data trace after 800 ms was also eliminated to ensure a consistent end time. The intervening 500-ms eye movement trace was filtered using a Savitzky-Golay finite impulse response smoothing filter (Holmqvist et al., 2011) to smooth out the noise in the signal. The trace was then divided into five 100-ms bins. In each bin, an average speed in the X direction was calculated by taking the difference between the X position of the first and last sample in the bin and dividing it by the difference in time. If the bin had any consecutive points where the rate of change in X position was greater than 30°/s, it was assumed that the bin contained another type of eye movement with a faster velocity profile (e.g., a saccade or blink) and this bin was discarded from the analysis. The value of 30°/s was chosen since the shortest saccades typically have velocity peaks of about 30°/s –40°/s (Holmqvist et al., 2011). Each participant therefore had up to 3,000 average smooth pursuit speed measurements from both comparison and standard trials (1,000 for each drift condition). On average, approximately 19% of these measurements for both standard and comparison targets were discarded from smooth pursuit analysis because they contained another type of eye movement according to these measures. For each trial, an average was taken for the smooth pursuit speed across all eligible measurements (up to five).

The smooth pursuit data were classified as a binary variable, being given a value of 0 if the average comparison smooth pursuit speed on a given trial was slower than the average standard smooth pursuit speed, and a value of 1 if the average comparison smooth pursuit speed was faster than the average standard smooth pursuit speed. This measure was then used to construct oculometric functions, analogous to psychometric functions, for the smooth pursuit data (Beutter & Stone, 1998; Kowler & McKee, 1987). In accordance with the perceptual PSEs, we defined OSEs as the speed at which the smooth pursuit to the comparison target was faster than that to the standard target on 50% of trials.

Modeling was carried out using generalized linear mixed models, as detailed in the Perceptual analysis section. The binary smooth pursuit variable was used as the dependent variable and trial drift type and stimulus speed were used as fixed factors. The random effects structure was the same as for the perceptual data.

To calculate the accuracy of smooth pursuit, the average velocity gain for each participant and drift type was calculated (by taking the average smooth pursuit speed as calculated using the 100-ms bins and dividing by the target speed) and was used as the dependent variable in a repeated-measures analysis of variance (ANOVA), with drift type as the independent variable. Post hoc comparisons were carried out using Tukey tests. A measure of position error was also taken for comparison trials; the eye location was subtracted from the target position for all the components of each trial calculated to be smooth pursuit (after downsampling the eye location data to match the temporal frequency of the stimulus presentation). A mean error value was then taken for each trial; a negative error meant the eye was behind the target, and a positive error meant it was in front of the target. Modeling was carried out using linear mixed models, with the mean error variable as the dependent variable and trial drift type as a fixed factor. The random effects structure was the same as for the previous analyses.

Other eye movement analysis

In addition to calculating smooth pursuit velocities, we also took measures of the saccades in each trace (Holmqvist et al., 2011): the total number, the peak velocity, the peak acceleration, and the direction (either in the direction of overall target motion or in the opposite direction). Saccades were identified by using a velocity- and acceleration-based algorithm based on the SensoMotoric Instruments (SMI) algorithm (Smeets & Hooge, 2003) and using parameter values recommended by Eyelink. First, all areas of the trace where the velocity exceeded a baseline threshold were found (taken to be 11°/s, determined by visually inspecting the traces and determining the threshold that produced a good fit to the perceived extent of saccades) at least once in a 6-ms period (this tolerance was built in to allow for noise in the velocity measurements). Saccades were identified from these areas by selecting only the regions in which the peak velocity was greater than 30°/s (but not larger than 900°/s: these periods were classified as blinks), the peak acceleration was greater than 8,000°/s^2 and the total length of the saccade was at least 10 ms. Approximately 5% of standard and stimulus traces contained a blink, and therefore were not used for further saccade analysis.

The average number of saccades (by block and participant) in the direction of motion (catch-up) in each comparison presentation and the average number of saccades in the direction opposite to motion (step-back) in each comparison presentation were used as dependent variables in two separate repeated-measures ANOVAs with drift type as the independent variable. Post hoc comparisons were carried out using Tukey tests. The average number of catch-up and step-back saccades for each participant and drift type ($n = 45$ for each saccade type) was also correlated with the OSE measures using Spearman's rank correlation coefficient.

Finally, the difference between the target position and the eye position immediately preceding and following each saccade was calculated for the comparison stimuli. These pre- and postsaccadic error measurements were used to consider whether there were differences in saccadic positional correction for the different drift types. A mixed effects model used the difference between post- and presaccadic errors as the dependent variable, and drift type as an independent variable. The random effects structure was the same as for the perceptual data.

Correlation between eye movement measures and perception analysis

For the smooth pursuit data, oculometric functions were compared against the perceptual data by correlating both the OSEs and the smooth pursuit velocity gain for the comparison stimuli with the PSEs ($n = 45$) using Spearman's rank correlation coefficient to determine if there were similarities between pursuit and perception. We also conducted trial-by-trial correlations of smooth pursuit and perceptual response data for each participant by correlating the binary perceptual responses against the average comparison smooth pursuit on each trial ($n =$ up to 600 trials per person), with the correlation between the smooth pursuit speed and the physical target speed partialed out (Gegenfurtner et al., 2003).

We also carried out analyses looking at the correlation between saccade measures and perception. Firstly, we analyzed whether there was any correlation between PSEs and the mean number of both catch-up and step-back saccades using Spearman's rank correlation coefficient. We did not attempt to model psychometric functions for these response measures as a significant proportion of trials did not contain saccades. Secondly, we analyzed the correlations between PSEs and the mean pre- and postsaccadic errors for each participant and condition, again using Spearman's rank correlation coefficient.

Finally, we asked whether including a saccade component in the calculation used to determine the oculometric function would lead to a higher correlation between the PSEs and the OSEs. Perceptual psychometric functions were fitted by iteratively finding the best μ and σ for a logistic curve with *fminsearch* in MATLAB, using the sum of squares as the parameter to be minimized. Oculometric functions were then fitted in a similar manner, except that instead of simply asking which of the two experimental epochs (standard or comparison) had the largest smooth pursuit value and assigning a binary variable on this basis, we added a component that included the number of catch-up saccades made in that presentation, multiplied by a factor α (step-back saccades were not included as these did not correlate significantly with perceptual PSEs) in the following manner:

$$\text{cue} = \text{smooth pursuit speed} + \alpha(\text{number of catch up saccades}) \quad (1)$$

The best value for α was found, again using an iterative search with *fminsearch*, and the measure of fit we attempted to minimize was (1 − Spearmann's rank correlation coefficient). If the standard cue value was greater than the comparison cue value, the response was given a value of 0; otherwise, it was given a value of 1.

Results

Preliminary experiment: Perceptual analysis

Figure 2 shows psychometric functions for the four participants who took part in the preliminary experiment, where they made perceptual judgments of speed while fixating a spot, as in previous studies (Hisakata et al., 2013; Lisi & Cavanagh, 2015; Shapiro et al., 2010; Zhang et al., 1993). If speed perception on this task had been veridical, the 50% point should correspond to a comparison speed of 8°/s (the same as the standard) and the no-drift condition does indeed show approximately this behavior. However, both of the drift conditions show shifts of the psychometric function for all participants; the forwards-drift condition curve is clearly shifted to the left, suggesting that this stimulus was perceived as faster than the standard, and the backwards-drift condition curve is clearly shifted to the right, suggesting that this stimulus was perceived as slower than the standard.

The final model of the data after model selection using log-likelihood procedures (Zuur et al., 2009) contained two fixed factors that both showed significant effects: speed ($\chi^2 = 282.41$, $df = 1$, $p < 0.001$) and stimulus drift type ($\chi^2 = 308.05$, $df = 2$, $p < 0.001$) There was no significant interaction of stimulus drift type and speed, and thus this interaction term was dropped from the final model. Post hoc tests using Tukey contrasts confirmed that there was a significant difference between all three drift types. The forwards-drift stimulus was perceived as moving faster than the no-drift stimulus ($Z = 13.15$, $p < 0.001$), whereas the backwards-drift stimulus was perceived as moving more slowly ($Z = -11.48$, $p < 0.001$). The forwards-drift and backwards-drift stimuli were also significantly different from each other ($Z = -17.54$, $p < 0.001$). Considering the aggregate PSEs across all participants also supports this conclusion; the PSE for the forwards-drift condition was lower than veridical (6.896°/s, or a 14% change from the no-drift condition). The opposite was true for the backwards-drift condition, where the PSE was higher than the true speed of the standard (8.895°/s, or an 11% change from the no-drift condition). This suggests that the effects are approximately equal and opposite for the two directions of drifting motion, and supports previous work suggesting that strong and consistent biases in speed judgments can be seen during fixation (Hisakata et al., 2013; Lisi & Cavanagh, 2015; Shapiro et al., 2010; Zhang et al., 1993).

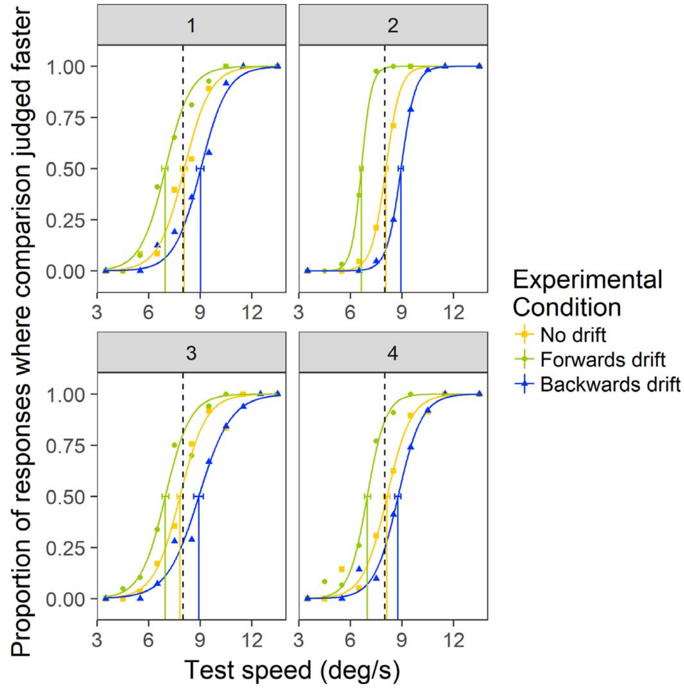

Figure 2. Perceptual results in the preliminary experiment showing individual psychometric functions for each participant. Points represent the proportion of responses where the comparison was judged faster at each speed. Lines represent the logistic fit by direct maximization of the likelihood, and the error bars reflect the parametric bootstrapped confidence intervals.

Main experiment: Perceptual analysis

The results in the top panel of Figure 3 show that there was a high degree of variability between participants' performance on the perceptual task when they pursued the targets rather than fixating a spot (Figure 3A). Some participants did show relatively strong perceptual speeding up for the forwards-drift case and perceptual slowing down for the backwards-drift case (e.g., Participants 3 and 9) while others actually showed effects in the opposite direction (e.g., Participants 5 and 8). The bottom panel (Figure 3B) shows the average psychometric functions for the different conditions across participants, and shows that there are relatively small differences between the different drift types on average, particularly for the backwards-drift and no-drift cases.

After model selection, the final model of the data contained only speed as a significant main effect ($\chi^2 = 498.95$, $df = 1$, $p < 0.001$). The nonsignificant effect of drift type in this model presumably reflects the individual differences in response. An exploratory

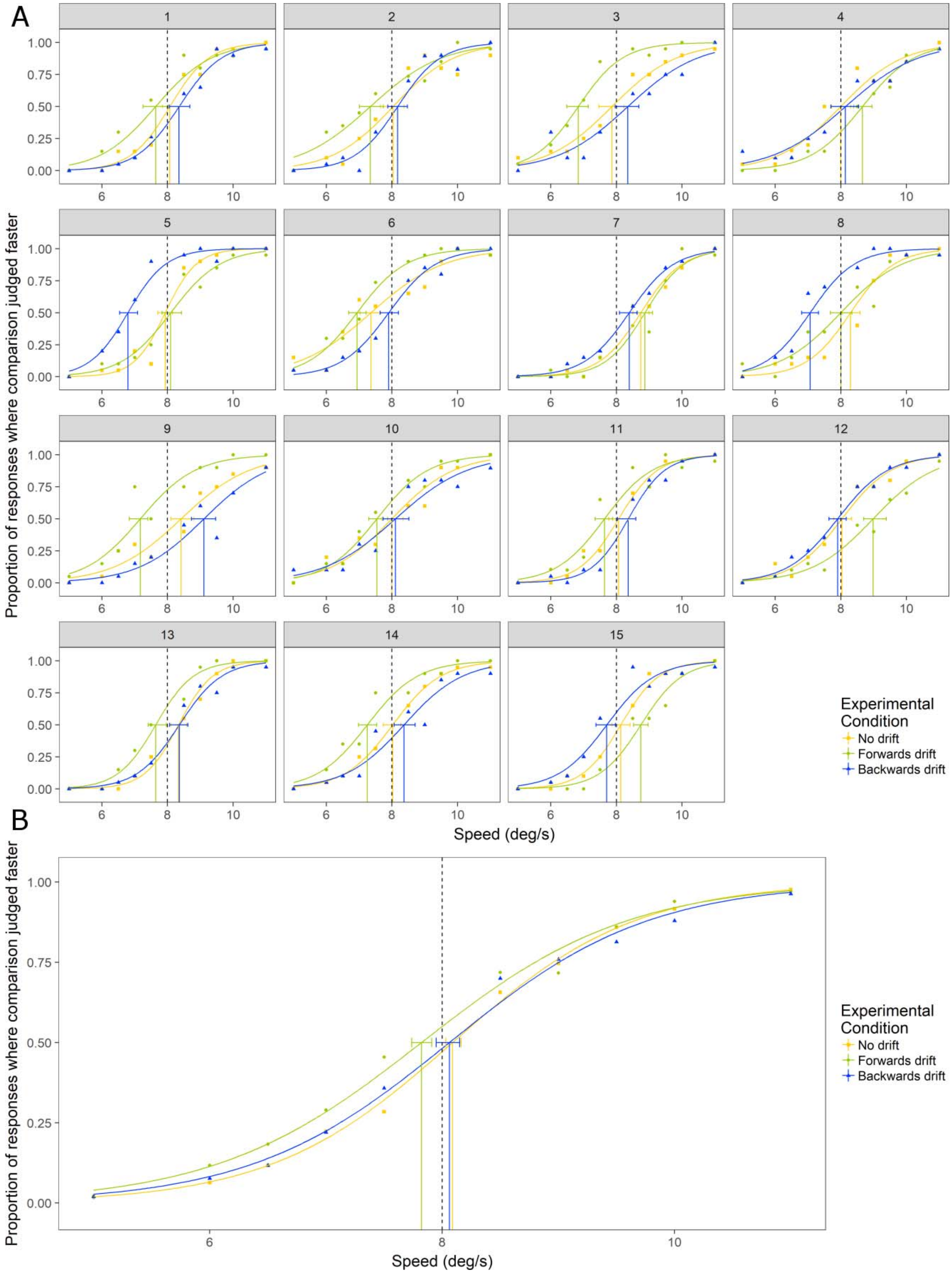

Figure 3. (A) Perceptual results in the main experiment showing individual psychometric functions for each participant. Points represent the proportion of responses where the comparison was judged faster at each speed. Lines represent the logistic fit by direct maximization of the likelihood, and the error bars reflect the parametric bootstrapped confidence intervals. The dotted lines show the standard speed. (B) Perceptual results in the main experiment showing the average psychometric functions for each condition across all participants.

model including gender showed a nonsignificant interaction of drift type with gender, indicating that this factor cannot explain the individual differences seen. Our results therefore showed no evidence for consistent biases in speed perception in this task.

Oculometric analysis

As can be seen from Figure 4, for the majority of participants, smooth pursuit velocity was clearly faster to the forward-drift target compared to the no-drift condition and slower to the backwards-drift target compared to the no-drift target.

On average, the OSE for the no-drift condition is approximately veridical, while the OSE for the forwards-drift condition is shifted to a lower value (indicating that there was a bias towards pursuing the comparison target more quickly than it was really moving; the bias is approximately 7% of the standard speed) and the PSE for the backwards-drift condition is shifted to a higher value (indicating that there was a bias of approximately 13% compared to the standard toward pursuing the comparison target more slowly). Internal motion of stripes therefore appears to bias the speed of smooth pursuit eye movements.

In the final general linear mixed model describing the oculometric data, there is a significant interaction between speed and drift type, indicating that there are differences in slope between the different drift types ($\chi^2 = 14.662$, $df = 2$, $p < 0.001$). This appears to be because the no-drift condition has a steeper slope than the other conditions.

While these analyses suggest that there are differences between the drift conditions, they do not indicate which (if any) drift types were pursued accurately. To address this, we calculated the mean velocity gain for each observer for the different drift types (Figure 5A). This analysis shows that the no-drift condition generally had a mean gain close to 1, indicating good tracking performance overall, whereas the forward-drift condition had a higher gain on average and the backwards-drift condition a lower gain on average. An ANOVA confirms that drift type is a significant factor in the model ($F = 29.193$, $p < 0.001$) and post hoc tests using Tukey comparisons show that all the drift types are significantly different from each other (no drift vs. backwards drift: $Z = 4.112$, $p < 0.001$; forwards drift vs. backwards drift: $Z = 7.633$, $p < 0.001$; forwards drift vs. no drift: $Z = 3.521$, $p = 0.001$). An analysis of the mean position error between the target and the eye during the smooth pursuit components of the comparison trials gave similar results (Figure 5B); in particular, post hoc Tukey tests showed that the forwards drift and backwards drift conditions were significantly different from each other ($Z = 10.781$, $p < 0.001$). There was also a significant difference between the forwards drift and no drift conditions ($Z = 7.251$, $p < 0.001$), and between the backwards drift and no drift conditions ($Z = -6.730$, $p = 0.323$).

Other eye movement analysis

As previous research has shown that there are different biases for saccades and smooth pursuit eye movements (Lisi & Cavanagh, 2015), we considered whether there were different saccadic responses for the different drift types. Figure 6 shows that for the backwards-drift stimuli, there were more saccades in the direction of overall motion (catch-up) while for the forwards drift stimuli, there were more saccades opposite to the direction of overall motion.

Drift type is a significant factor in the model for both the measure of the number of catch-up saccades ($F = 45.771$, $df = 2$, $p < 0.001$) and for the number of step-back saccades ($F = 34.166$, $df = 2$, $p < 0.001$). Post hoc comparisons carried out using Tukey tests suggest that in the case of catch-up saccades there are significant differences between all three drift types, with backwards-drift targets having the largest number of these types of saccade, followed by the no-drift target and finally the forwards-drift target (forwards drift vs. no drift: $Z = -4.002$, $p = 0.001$ and no drift vs. backwards drift: $Z = -5.525$, $p < 0.001$). For step-back saccades there is a significant difference between the no-drift and backwards-drift targets ($Z = 2.581$, $p = 0.027$), with the no-drift condition having a greater number of step-back saccades. Similarly, there is a significant difference between the no-drift and the forwards-drift targets ($Z = 5.510$, $p < 0.001$), with the forwards-drift condition having a larger number of step-back saccades than the no-drift condition. In contrast to the smooth pursuit responses, which tended to bias the eye away from the target in the same direction as the internal drift, saccades were more likely to be in the opposite direction to the internal drift of the target.

Supporting these findings, there is also significant positive correlation between the number of catch-up saccades and the OSEs ($\rho = 0.648$, $p < 0.001$) and a significant negative correlation between the number of step-back saccades and the OSEs ($\rho = -0.640$, $p < 0.001$). This is consistent with the notion that smooth pursuit is slower than veridical to the backwards-drift stimuli, necessitating more catch-up saccades (Butzer et al., 1997), while smooth pursuit is faster than veridical to the forwards-drift stimuli, leading to more step-back saccades.

Finally, we considered how the position of the eye changed from just before the saccade to just following the saccade in the different drift type conditions. As can be seen in Figure 7, the saccades tend to act in the opposite direction to the position biases generated during smooth pursuit; the eye generally falls behind the target in both the no-drift and backwards-drift

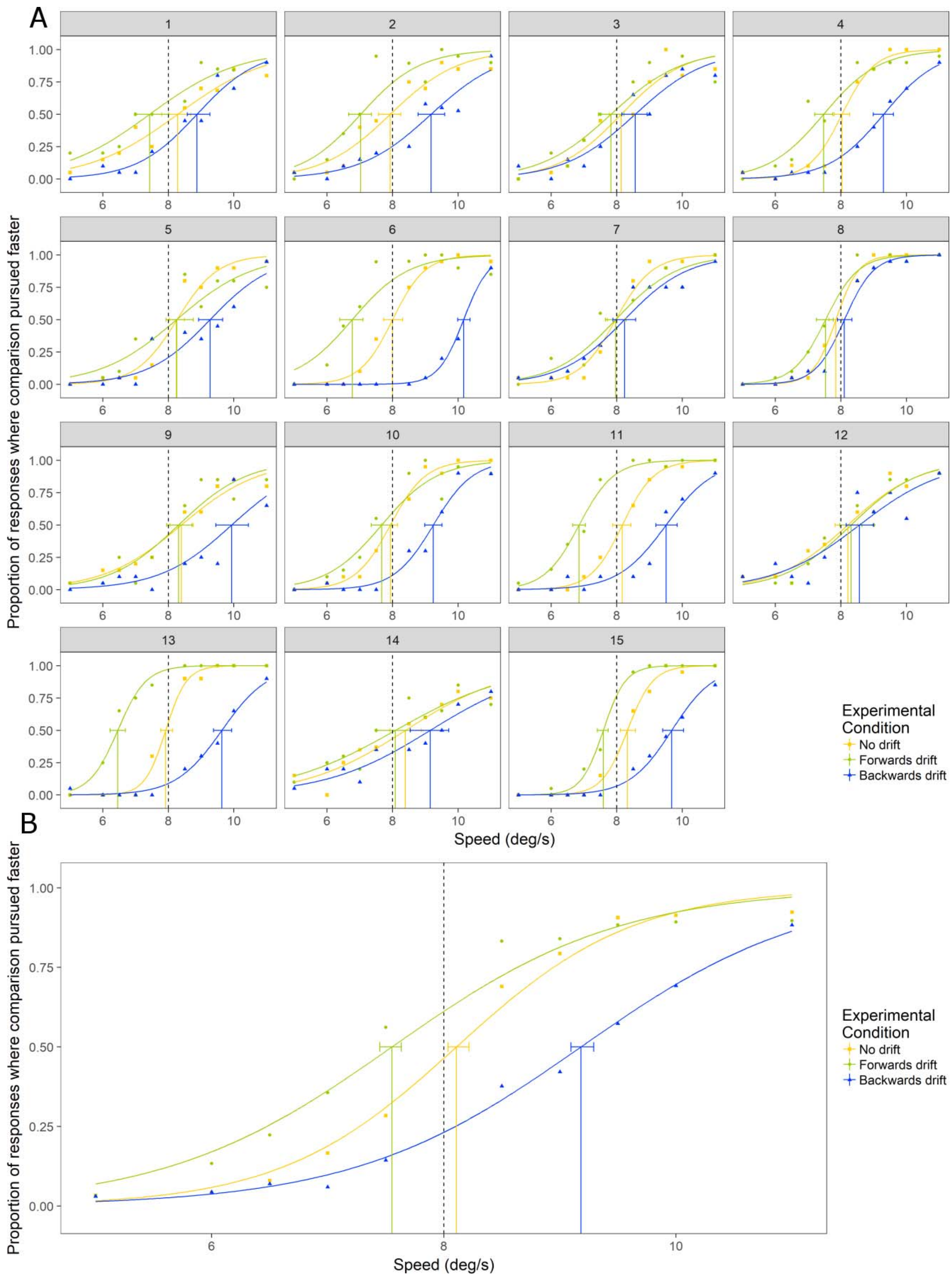

Figure 4. (A) Oculometric results in the main experiment showing individual psychometric functions for each participant. Points represent the proportion of responses where the comparison was pursued faster than the standard at each speed. Lines represent the logistic fit by direct maximization of the likelihood, and the error bars reflect the parametric bootstrapped confidence intervals. The dotted lines show the standard speed. (B) Oculometric results in the main experiment showing the average oculometric functions for each condition across all participants.

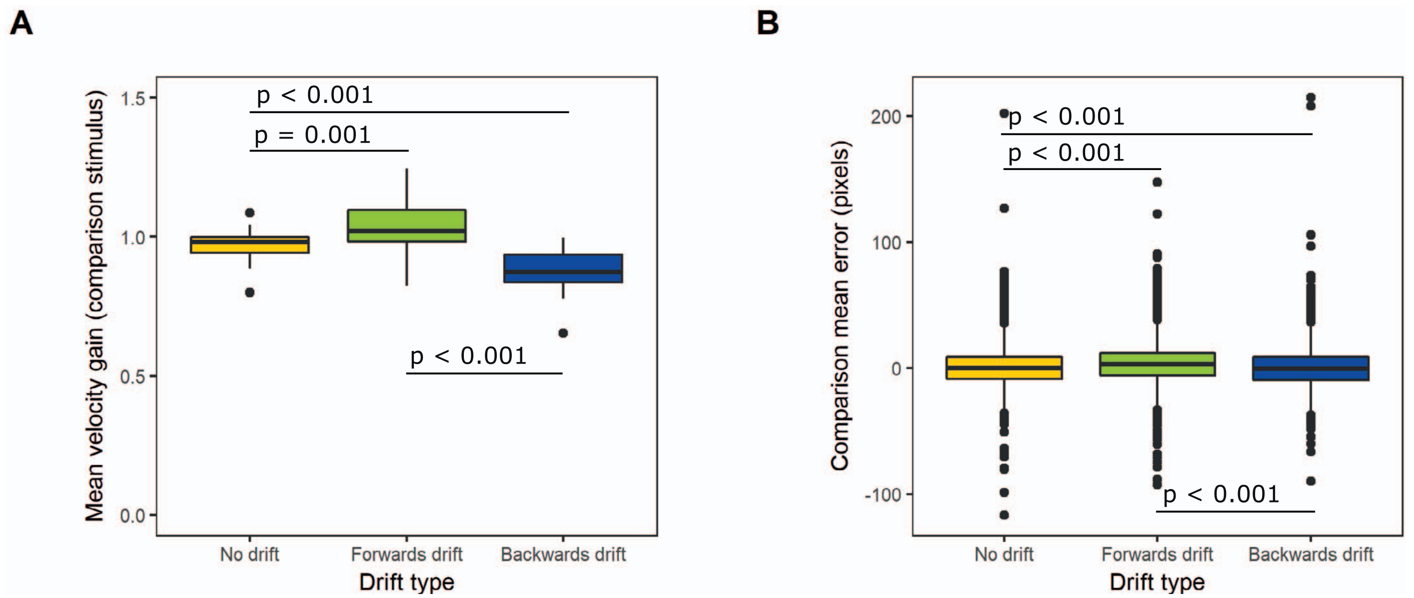

Figure 5. (A) Box plot to show the average comparison stimulus smooth pursuit gain in 500 ms for the different trial types (each of the 15 participants contributes one data point to each box). (B) Box plot to show the comparison mean error in pixels for the different trial types (each dot represents an individual trial). In both plots, whiskers encompass 1.5× the interquartile range, and points beyond this are plotted as outliers (black circles). Medians are represented by black lines.

conditions, and is then frequently moved ahead of the center of the target after the saccade. There seem to be more individual differences in the forwards-drift condition, but there is a greater tendency for the movement to be in the opposite direction. Interestingly, there is also a tendency to overcompensate; for many participants, the saccades do not reduce the error, but instead switch it to the opposite direction.

Post hoc Tukey tests carried out on a model using the difference between the pre- and postsaccade errors as a dependent variable suggests that all three drift types have different patterns of position adjustments by saccades. The error for the positive-drift condition is significantly more negative than the no-drift condition ($Z = -12.673$, $p < 0.001$), indicating that the eye is displaced further behind the target following saccades

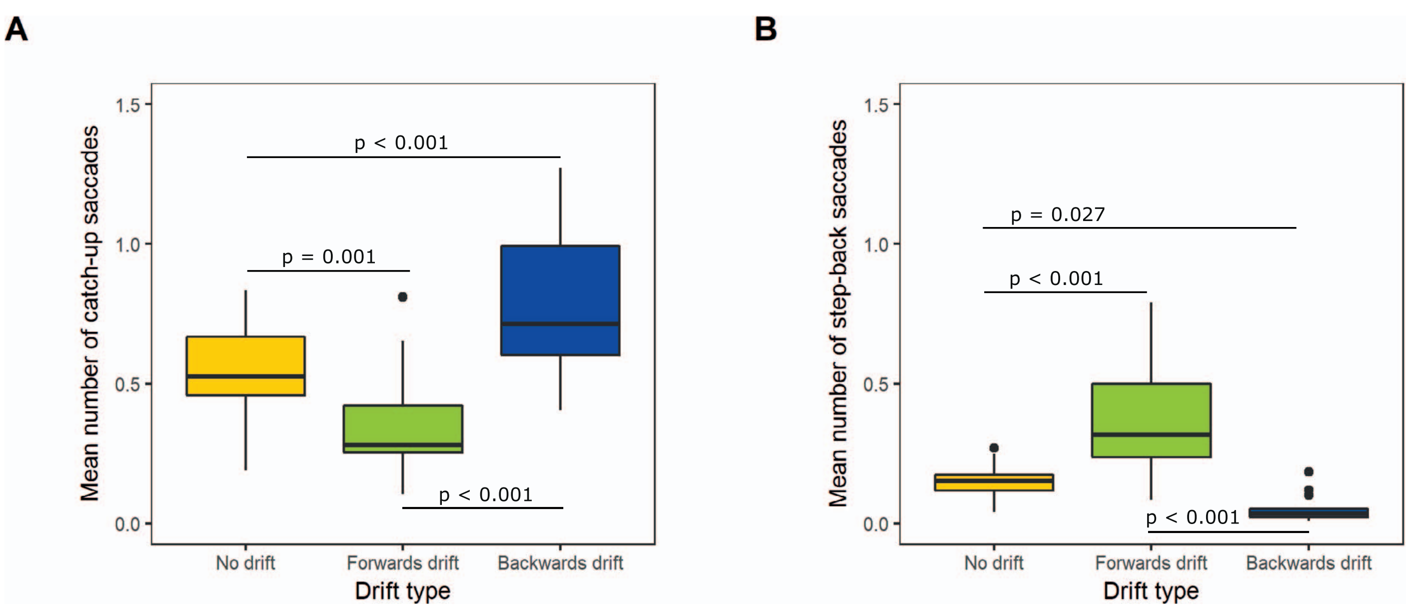

Figure 6. Box plot to show mean numbers of saccades in 500 ms for the different trial types (each of the 15 participants contributes one data point to each box). Whiskers encompass 1.5× the interquartile range, and points beyond this are plotted as outliers (black circles). Medians are represented by black lines. (A) Catch-up saccades. (B) Step-back saccades.

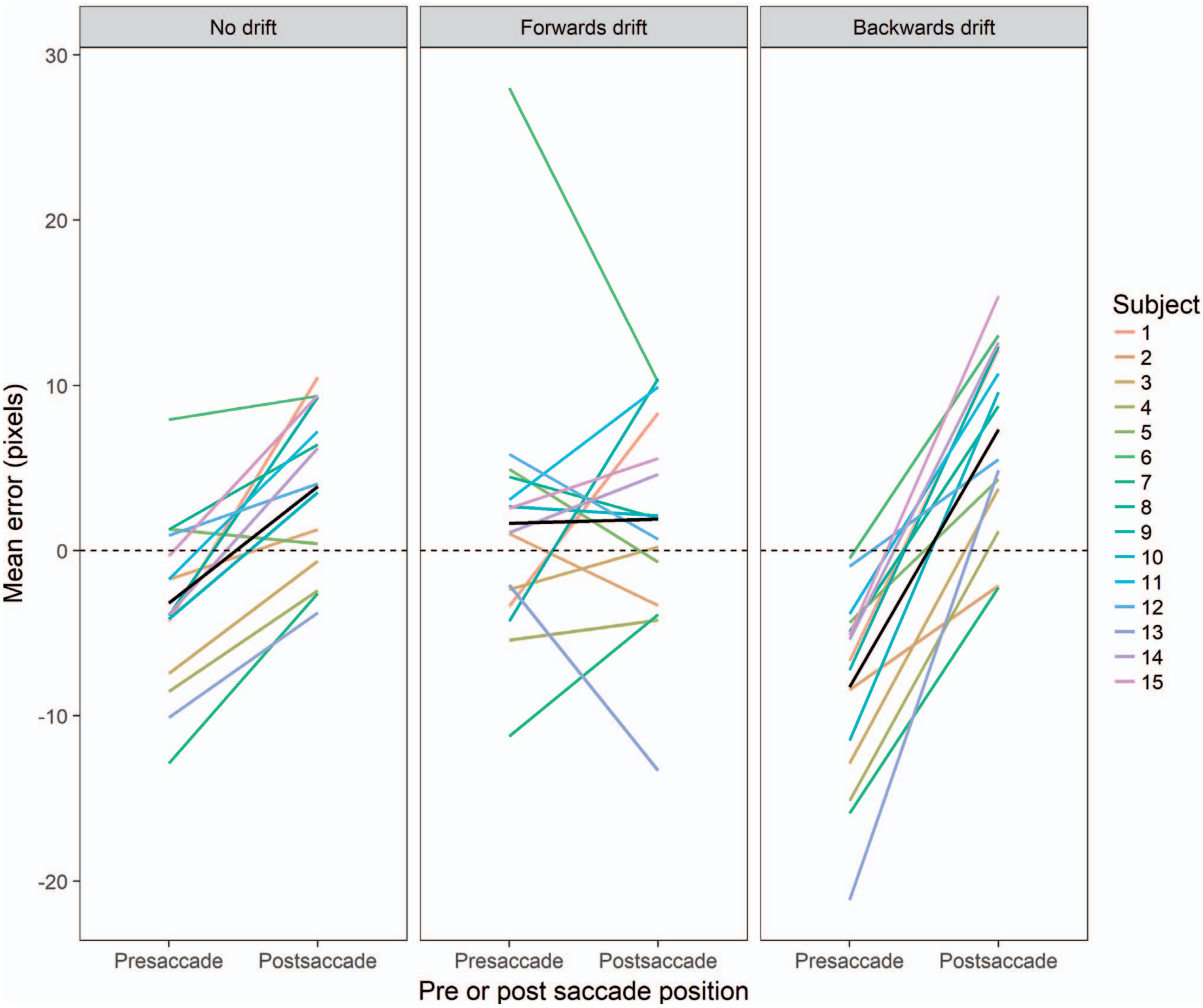

Figure 7. Graph to show how the eye position for each subject changed from pre- to postsaccade. Each panel represents one drift type condition, and each cultured line represents the difference between the two points for one subject (which were calculated by taking the mean error; e.g., on each trial, each pre- and postsaccade position was subtracted from the target position, and these values were averaged across the trial if more than one saccade was present on the trial, and across conditions). A positive mean error means the eye is in front of the target center, whereas a negative mean error means the target is behind the target center. The black lines represent the average difference between pre- and postsaccade position across subjects. The black dashed line is a reference line showing zero mean error.

in the positive-drift condition. However, the error for the backwards-drift condition is significantly more positive than the no-drift condition ($Z = 9.907$, $p < 0.001$), meaning that the eye is displaced further in front of the target following saccades in backwards-drift trials.

Relationship between eye movement and perceptual measures

To test the similarity between smooth pursuit and perception, we calculated the correlations between the perceptual PSEs and the smooth pursuit OSEs. Figure 8A shows that there is no correlation between these measures ($\rho = 0.287$, $p = 0.056$). This indicates that there is no significant trend for participants with higher PSEs to also have higher OSEs. Similarly, there is no significant relationship between the perceptual PSE and the average velocity gain of smooth pursuit ($\rho = -0.239$, $p = 0.114$; Figure 8B), again suggesting that the smooth pursuit eye movement measures are not related to the perceptual reports.

The above analyses only consider the responses of each participant on aggregate for each experimental condition. We therefore asked whether there was any

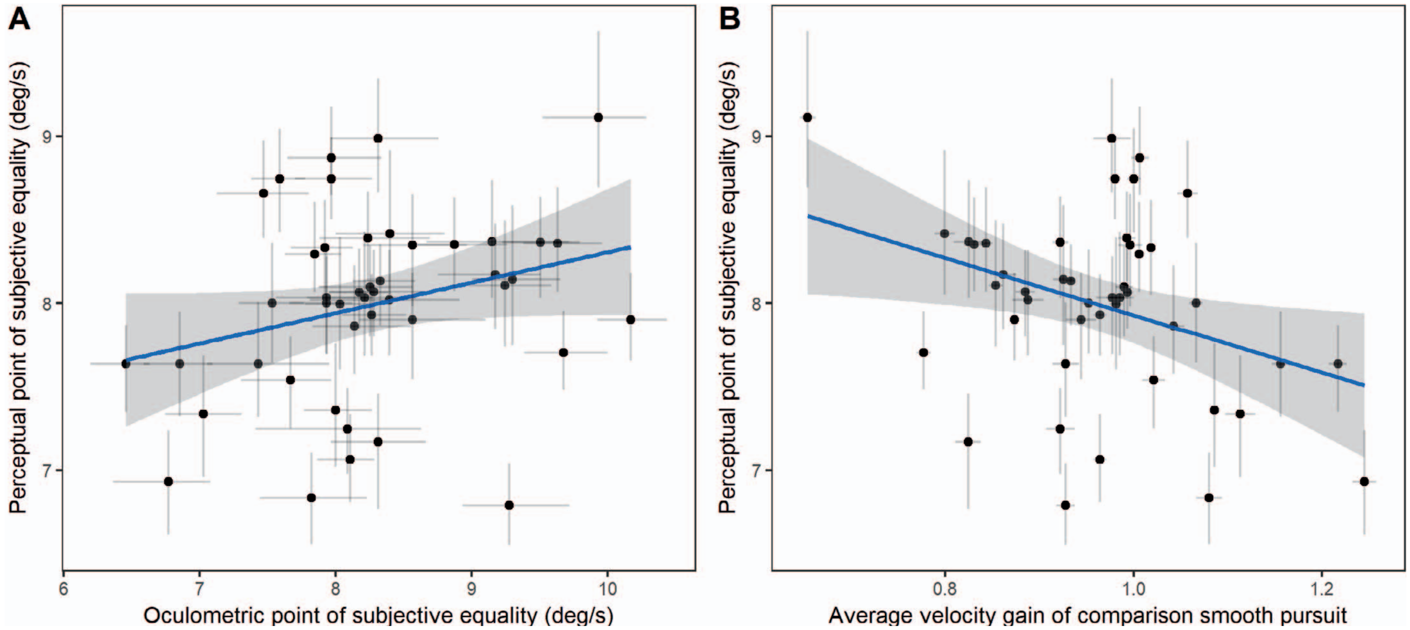

Figure 8. Each of the 15 participants contributes three points to each graph (one for each drift type). (A) Graph to show the OSEs plotted against the PSEs for each participant and drift type. *X* error bars represent the bootstrapped confidence intervals for the OSEs, and the *Y* error bars represent the bootstrapped confidence intervals for the perceptual PSEs. (B) Graph to show the average velocity gain of the comparison trial smooth pursuit plotted against the PSEs for each participant and drift type. *X* error bars represent the standard error of the mean for the velocity gain measurements, and the *Y* error bars represent the bootstrapped confidence intervals for the perceptual PSEs.

trial-by-trial correlation between perceptual responses and smooth pursuit OSEs. All participants showed very weak correlations on this measure (Subject 1: $r = 0.068$, Subject 2: $r = 0.030$, Subject 3: $r = 0.070$, Subject 4: $r = 0.003$, Subject 5: $r = 0.019$, Subject 6: $r = 0.132$, Subject 7: $r = -0.058$, Subject 8: $r = -0.031$, Subject 9: $r = 0.051$, Subject 10: $r = 0.025$, Subject 11: $r = 0.135$, Subject 12: $r = -0.034$, Subject 13: $r = 0.106$, Subject 14: $r = 0.074$, Subject 15: $r = -0.028$). These results confirm that there is no relationship between smooth pursuit speed and perceptual responses on this task, either overall or during a specific trial.

As we found no strong correlations between smooth pursuit and perception, we asked whether there were any correlations between perception and the number of saccades. The average number of catch-up saccades shows a significant correlation with the PSEs ($\rho = 0.365$, $p = 0.014$, see Figure 9A), with the PSEs getting larger (i.e., the target is perceived as moving slower) as the average number of saccades increases. The correlation between the number of step-back saccades and the PSEs is nonsignificant ($\rho = -0.183$, $p = 0.230$, see Figure 9B).

We also considered whether the PSEs correlated with measures of pre- and postsaccadic error. There was no significant correlation between postsaccadic error and PSEs ($\rho = -0.096$, $p = 0.531$; see Figure 9D). However, there was a significant negative correlation between presaccadic error and the PSEs ($\rho = -0.396$, $p = 0.008$; see Figure 9C), suggesting that the more negative the error between target and eye position before the saccade, the slower the subjective perception of the target. This relationship remained significant even after the removal of the most extreme point in Figure 9C.

The higher correlation coefficients of the PSEs with the saccade measures compared to the smooth pursuit measures led us to ask whether including a saccade component in the calculation used to determine the oculometric function would lead to a higher correlation between the PSEs and the OSEs. To do this, we used an iterative search method. With a factor alpha (Equation 1) fixed at zero (giving no contribution of catch-up saccades), we found a correlation coefficient $\rho = 0.241$. This is similar to the result in the previous section ($\rho = 0.287$), where the PSEs and OSEs were generated using a different procedure. By allowing α to vary, the largest ρ obtained was 0.359 for an $\alpha = 1.08$. This suggests that including a contribution from catch-up saccades can improve the relationship between perceptual and oculometric (smooth pursuit) measures. However, it did not improve the correlation coefficient compared to simply plotting PSEs against the mean number of catch-up saccades for that participant and condition.

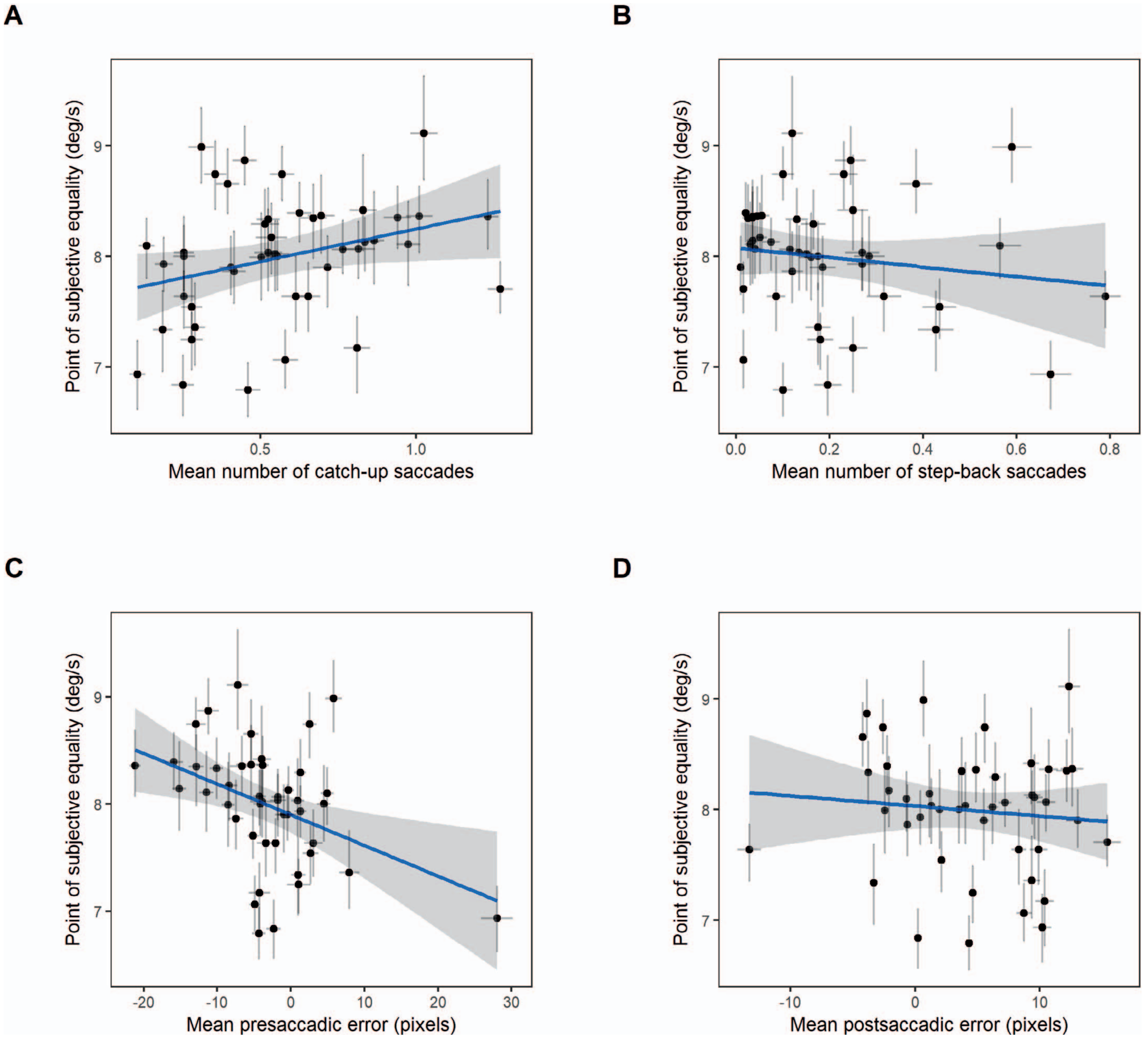

Figure 9. Graphs to show correlations between saccadic measures and PSEs for each participant and drift type. Each participant contributes three points to each graph (one for each drift type). *X* error bars represent the standard error of the mean, and the *Y* error bars represent the bootstrapped confidence intervals for the PSEs. Saccadic measures: (A) mean number of catch-up saccades, (B) mean number of step-back saccades, (C) mean presaccadic error, and (D) mean postsaccadic error.

Discussion

The results of the main eye tracking experiment show that there are clear differences in pursuit eye movements made to moving targets with different types of internal drift. Smooth pursuit to targets with internal drift opposite to the direction of the overall motion (backwards drift) is slower than that to targets with internal drift in the same direction as overall motion (forwards drift), and the eye is also displaced further back from the target center in the backwards-drift condition. In addition, participants make more catch-up saccades for backwards-drift targets and more step-back saccades for forwards-drift targets.

However, perceptual judgments in the same trials show a very different pattern compared to smooth pursuit eye movements, with participants showing smaller and more variable biases in perception for the different drift conditions (Figure 3). This contrasts with the strong biases shown during fixation in our preliminary experiment (Figure 2) and in previous literature (Shapiro et al., 2010; Zhang et al., 1993). We find that perception correlates more strongly with some saccadic measures, such as the number of catch-up saccades and the position of the eye before the initiation of a saccade. The relationship between perception and action in this study therefore seems to be complex, and to depend upon the measure of visual action used.

Dissociations between pursuit and perception

When considering smooth pursuit parameters, we found not only no trial-by-trial correlation between perception and pursuit, in common with previous studies on speed perception judgments (Braun et al., 2006; Gegenfurtner et al., 2003), but also no qualitative agreement between the two metrics: There is only a weak relationship between the PSEs for the perceptual data and the OSEs for the oculometric data or the smooth pursuit gain measures, suggesting that the individual differences seen in perception are not mirrored in the smooth pursuit speed. Previous research has often shown similarities between these two measures (Gegenfurtner et al., 2003; Kowler & McKee, 1987; Mukherjee et al., 2015), but our results support an increasing body of literature suggesting that despite these similarities, pursuit and perception can be dissociated (Braun et al., 2008; Gegenfurtner et al., 2003; Tavassoli & Ringach, 2010).

In a previous study where both stimulus and background could be perturbed in speed, the smooth pursuit velocity was determined by the motion average (Spering & Gegenfurtner, 2007). The results from our experiment are also consistent with the idea that overall movement speed and the internal drift speed were being averaged for the smooth pursuit response, with the speed increasing when the internal drift was in the same direction as the overall trajectory of motion and decreasing when it was opposite to the direction of motion. These findings also fit with other studies exploring the effect of briefly perturbing moving context velocity on smooth pursuit velocity (Kodaka, Miura, Suehiro, Takemura, & Kawano, 2004; Lindner, Schwarz, & Ilg, 2001; Spering & Gegenfurtner, 2007; Suehiro et al., 1999) and with results that suggest constant background motion speeds up smooth pursuit velocity when it is in the direction of target motion and slows it down when it is opposite to target motion (Masson, Proteau, & Mestre, 1995).

However, the results for speed perception in our main experiment were much less clear cut. If the visual system was able to subtract the context motion from the overall target motion completely, as per Spering and Gegenfurtner's (2007) results, it would be expected that both types of drift would be perceived veridically or with an opposite effect. It appears that on average, participants were able to subtract the drift out from their overall perception of target motion, leading to near veridical speed estimates. However, this averaging process hides a great deal of individual variability. While some participants were able to segregate the overall speed of the target from the internal motion, allowing them to make near veridical speed estimates, others seemed to be biased by the internal motion of the stripes.

It is possible that some of the variation in speed perception seen in our experiment could be explained by what participants take as their reference for the relative, background motion used to generate motion contrast. Participants who track the overall movement of the target may be more likely to perceive the target speed veridically, given that the background in this case is stationary in the real world (and therefore moving in the expected opposite direction and speed on the retina). On the other hand, if participants use the internal stripe motion as a type of background motion with which to compare the target motion, their speed perception may be biased. Previous work has also suggested that when participants make velocity judgments in the context of a moving background, both retinal (the motion of the surround relative to the target) and extraretinal (e.g., copies of the instructions being used to drive eye muscles) signals appear to be used, and that there are individual differences in when they are used and how they are combined (Brenner & van den Berg, 1994). Some of the idiosyncrasies in participant response in our experiment may therefore relate to differences in the use of retinal and extraretinal rotation information.

Speed judgments during fixation versus pursuit

One interesting finding in the current study is the large difference between speed judgments when participants fixated compared to when they pursued the target. During fixation, the perceptual results showed a relatively large, consistent, and approximately symmetrical bias away from the true veridical speed (very similar to the smooth pursuit speed biases seen in the main experiment). However, when participants tracked the target, a much greater degree of variability in perceptual judgments was seen between participants. One explanation for the differences seen during fixation and pursuit may relate to the motion contrast versus integration distinction discussed previously (Spering & Gegenfurtner, 2007). Previous research has shown that increasing eccentricity increases the chance of motion integration (Zhang et al., 1993), and much of the trajectory of the target would have been seen using peripheral vision during the fixation task.

An alternative explanation for why the perceptual biases were less strong during tracking is that pursuit eye movements inherently provide less reliable sensory evidence; the Aubert-Fleischl effect shows that people who fixate on a point perceive stimuli as moving more quickly compared to people who are pursuing them, and this has been argued to reflect an increased reliance on prior expectations within a Bayesian framework (Freeman, Champion, & Warren, 2010). While our data are consistent with the notion that speed judgments are harder to make while pursuing, given that the psychometric curves for the main experiment are on average shallower than those seen in the preliminary experiment, this does not necessarily explain the wide range of individual biases for the different trial types seen in our main experiment. We suggest that the relatively large sample size used in this experiment should allow us to overcome this noise and see any systematic biases if they were indeed present.

There have been other recent findings that suggest possible dissociations between eye movements and perception during fixation and tracking. In one study, participants were asked to attempt to intercept a moving target with their finger (de la Malla, Smeets, & Brenner, 2017). Internal motion of the target pattern (similar to that used in the present experiment) led to biases in interception when the participants were instructed to fixate, but these biases were much reduced when they were able to track the target. In addition, the smooth pursuit gain showed similar biases to the interception errors at fixation, but not when tracking. This result supports the current study's findings, and suggests that perceptual judgments made during fixation may not always reflect those seen in a more naturalistic tracking task.

However, not all experiments have shown reduced illusory biases when tracking. In one study, dynamic stripe patterns moving in the same direction as the target tended to increase the perceived speed of the target, whereas patterns moving in the opposite direction to the target tended to decrease the perceived speed (Hall et al., 2016). While there were many differences in design between this study and ours that could explain the differences in results seen, it is worth noting that individual data were not presented in Hall et al.'s study, and therefore it is difficult to assess the across-participant variability, which could have been substantial. In addition, there were relatively high numbers of excluded participants in Hall et al.'s study (up to nearly 40% of the participants tested in one experiment). We suggest that individual differences may therefore previously have been underestimated in this task.

The role of saccadic eye movements

While we have primarily considered smooth pursuit as an example of an oculomotor action in this study, it may be simplistic to always assume a unitary dissociation between action and perception. In one direction perception task, smooth pursuit and perception were shown to have similar illusory biases, but saccades targeted veridical locations (Lisi & Cavanagh, 2015). Similarly, it also has recently been shown that context motion can affect eye and hand movement latency but does not affect interception accuracy (Kreyenmeier, Fooken, & Spering, 2017).

We therefore also considered whether saccadic measures correlated more closely with perceptual data. Human participants frequently make saccadic eye movements during tracking tasks, particularly at faster speeds or with irregular target trajectories (Collewijn & Tamminga, 1984), and previous research has suggested that both catch-up and step-back saccades can be seen in smooth pursuit responses to second order motion (Butzer et al., 1997). In our task, we found that the number of catch-up saccades correlated with the PSEs, with an increased number of these saccades being seen when there was a higher PSE (and thus a slower perceived speed). This seems to reflect better correlation of the backwards-drift stimuli, which is perhaps unsurprising given that catch-up saccades are most prevalent for these trials.

One possible explanation is that participants who showed a greater number of catch-up saccades to the backwards-drift stimuli may have been tracking the internal drift more closely, as this would displace the eye further back than the real trajectory, perhaps necessitating catch-up saccades and simultaneously leading to slower speed judgments. This explanation fits with previous studies, which have shown that movement of the background opposite to that of the target motion in smooth pursuit tasks produces more catch-up saccades (Masson et al., 1995). Participants who showed fewer catch-up saccades on the backwards-drift trials in our experiment tended to have lower PSEs, perhaps suggesting that they were better able to track the overall motion of the target veridically, segregating the target out from the stationary background and therefore reducing their bias towards seeing the backwards-drift stimulus as moving more slowly. The relationship between catch-up saccades and perception could therefore act as an indication of the strategy that the participant is using to complete the task. The evidence therefore does not suggest that the catch-up saccades act as a mechanism to correct perceptual biases, as if this were the case, it might be expected that participants with a greater number of catch-up saccades would show more veridical PSEs.

We also found that the presaccadic error between eye and target correlated with the perceptual judgments made by participants, but the postsaccadic error did not. The negative relationship between presaccadic error and participant's point of subjective equality suggests that the further back the eye was displaced before the saccade, the greater the likelihood that the target would be perceived relatively slowly. This may be a consequence of increased motion integration in these participants, as the target is perceived further into the periphery (Zhang et al., 1993), although it is then perhaps surprising that the postsaccadic error did not also show a significant relationship with perception. Instead, this may again be a consequence of the tracking strategy used the participant; participants who tracked the internal motion more closely may have been more likely to have their eyes displaced further behind the target shortly before a saccade, and were also more likely to judge the target to be slower.

Limitations and future work

One limitation of the current study is that it focused only on the steady-state phase of tracking, with analysis beginning 300 ms into the trial. We did not consider the earlier, open-loop phase of tracking because our experimental set-up was not designed to specifically measure perceptual responses during this period of the trial. However, this would be an interesting avenue for further study, given that previous studies have found differences in speed estimation and discrimination for different phases of pursuit (Rasche & Gegenfurtner, 2009; Wilmer & Nakayama, 2007), perhaps leading to a stronger relationship between pursuit and perception during the open-loop phase where pursuit may be less affected by extra-retinal signals.

Conclusions

We consider the relationship between perception and eye movements in a speed perception task using moving Gabors with internal drift. While smooth pursuit eye movements showed biases reflecting speed averaging of the carrier and envelope motion, perceptual responses during tracking were much more variable, perhaps suggesting that different participants used different strategies to complete the perceptual task. While smooth pursuit speed showed no significant correlations with perceived speed, the average number of catch-up saccades observed and the difference in position between the target and the eye immediately before a saccade did correlate with perception. This indicates that the type of visual action studied is key in determining the relationship with perception.

Keywords: smooth pursuit, *motion perception*, *speed perception*, *saccades*

Acknowledgments

The author would like to thank Martha Fawcett for assistance with the preliminary experiments and David Tolhurst for helpful discussions throughout the project and comments on the manuscript. This work was supported by a studentship from the Biotechnology and Biological Sciences Research Council (BBSRC)/UK (BB/F016581/1) and a CASE award from Defence Science and Technology Laboratory (Dstl).

Commercial relationships: none.
Corresponding author: Anna E. Hughes.
Email: a.hughes2@exeter.ac.uk.
Address: Centre for Life and Environmental Sciences, University of Exeter, Penryn, UK.

References

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *ArXiv*:1406.5823 [Stat]. Retrieved from http://arxiv.org/abs/1406.5823

Beutter, B. R., & Stone, L. S. (1998). Human motion perception and smooth eye movements slow similar directional biases for elongated apertures. *Vision Research*, *38*(9), 1273–1286, https://doi.org/10.1016/S0042-6989(97)00276-9.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.

Braun, D. I., Mennie, N., Rasche, C., Schütz, A. C., Hawken, M. J., & Gegenfurtner, K. R. (2008). Smooth pursuit eye movements to isoluminant targets. *Journal of Neurophysiology*, *100*(3), 1287–1300, https://doi.org/10.1152/jn.00747.2007.

Braun, D. I., Pracejus, L., & Gegenfurtner, K. R. (2006). Motion aftereffect elicits smooth pursuit eye movements. *Journal of Vision*, *6*(7):1, 671–684, https://doi.org/10.1167/6.7.1. [PubMed] [Article]

Brenner, E., & van den Berg, A. V. (1994). Judging object velocity during smooth pursuit eye movements. *Experimental Brain Research*, *99*(2), 316–324, https://doi.org/10.1007/BF00239598.

Butzer, F., Ilg, U. J., & Zanker, J. M. (1997). Smooth-pursuit eye movements elicited by first-order and second-order motion. *Experimental Brain Research*, *115*(1), 61–70.

Cavanagh, P., Tyler, C. W., & Favreau, O. E. (1984). Perceived velocity of moving chromatic gratings. *Journal of the Optical Society of America A*, *1*(8), 893–899, https://doi.org/10.1364/JOSAA.1.000893.

Collewijn, H., & Tamminga, E. P. (1984). Human smooth and saccadic eye movements during voluntary pursuit of different target motions on different backgrounds. *The Journal of Physiology*, *351*, 217–250.

de la Malla, C., Smeets, J. B. J., & Brenner, E. (2017). Potential systematic interception errors are avoided when tracking the target with one's eyes. *Scientific Reports*, *7*(1), 10793, https://doi.org/10.1038/s41598-017-11200-5.

Freeman, T. C. A., Champion, R. A., & Warren, P. A. (2010). A Bayesian model of perceived head-centered velocity during smooth pursuit eye movement. *Current Biology*, *20*(8), 757–762, https://doi.org/10.1016/j.cub.2010.02.059.

Gegenfurtner, K. R., & Hawken, M. J. (1996a). Interaction of motion and color in the visual pathways. *Trends in Neurosciences*, *19*(9), 394–401, https://doi.org/10.1016/S0166-2236(96)10036-9.

Gegenfurtner, K. R., & Hawken, M. J. (1996b). Perceived velocity of luminance, chromatic and non-Fourier stimuli: Influence of contrast and temporal frequency. *Vision Research*, *36*(9), 1281–1290.

Gegenfurtner, K. R., Xing, D., Scott, B. H., & Hawken, M. J. (2003). A comparison of pursuit eye movement and perceptual performance in speed discrimination. *Journal of Vision*, *3*(11):19, 865–876, https://doi.org/10:1167/3.11.19. [PubMed] [Article]

Hall, J. R., Cuthill, I. C., Baddeley, R., Attwood, A. S., Munafò, M. R., & Scott-Samuel, N. E. (2016). Dynamic dazzle distorts speed perception. *PLoS One*, *11*(5), e0155162, https://doi.org/10.1371/journal.pone.0155162.

Hawken, M. J., & Gegenfurtner, K. R. (2001). Pursuit eye movements to second-order motion targets. *Journal of the Optical Society of America, A: Optics, Image Science, and Vision*, *18*(9), 2282–2296.

Hisakata, R., Terao, M., & Murakami, I. (2013). Illusory position shift induced by motion within a moving envelope during smooth-pursuit eye movements. *Journal of Vision*, *13*(12):21, 1–12, https://doi.org/10.1167/13.12.21. [PubMed] [Article]

Holmqvist, K., Nyström, M., Andersson, R., Dewhurst, R., Jarodzka, H., & van de Weijer, J. (2011). *Eye tracking: A comprehensive guide to methods and measures*. Oxford, UK: Oxford University Press.

Hughes, A., Fawcett, M., & Tolhurst, D. (2015). Measuring the effect of internal motion of a moving Gabor on speed perception and smooth pursuit. *Journal of Vision*, *15*(12):281, https://doi.org/10.1167/15.12.281. [Abstract]

Ihaka, R., & Gentleman, R. (1996). R: A language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, *5*(3), 299, https://doi.org/10.2307/1390807.

Kodaka, Y., Miura, K., Suehiro, K., Takemura, A., & Kawano, K. (2004). Ocular tracking of moving targets: Effects of perturbing the background. *Journal of Neurophysiology*, *91*(6), 2474–2483, https://doi.org/10.1152/jn.01079.2003.

Kowler, E., & McKee, S. P. (1987). Sensitivity of smooth eye movement to small differences in target velocity. *Vision Research*, *27*(6), 993–1015, https://doi.org/10.1016/0042-6989(87)90014-9.

Kreyenmeier, P., Fooken, J., & Spering, M. (2017). Context effects on smooth pursuit and manual interception of a disappearing target. *Journal of Neurophysiology*, *118*(1), 404–415, https://doi.org/10.1152/jn.00217.2017.

Krukowski, A. E., & Stone, L. S. (2005). Expansion of direction space around the cardinal axes revealed by smooth pursuit eye movements. *Neuron*, *45*(2), 315–323, https://doi.org/10.1016/j.neuron.2005.01.005.

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2014). lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects oflme4 package) (Version 2.0-11). Retrieved from http://CRAN.R-project.org/package=lmerTest

Linares, D., & Lopez-Moliner, J. (2016). quickpsy: An R package to fit psychometric functions for multiple groups. *The R Journal*, *8*(1), 122–131. Retrieved from http://journal.r-project.org/archive/2016/RJ-2016-008/index.html

Lindner, A., Schwarz, U., & Ilg, U. J. (2001). Cancellation of self-induced retinal image motion during smooth pursuit eye movements. *Vision Research*, *41*(13), 1685–1694, https://doi.org/10.1016/S0042-6989(01)00050-5.

Lisi, M., & Cavanagh, P. (2015). Dissociation between the perceptual and saccadic localization of moving objects. *Current Biology*, *25*(19), 2535–2540, https://doi.org/10.1016/j.cub.2015.08.021.

Masson, G., Proteau, L., & Mestre, D. R. (1995). Effects of stationary and moving textured backgrounds on the visuo-oculo-manual tracking in humans. *Vision Research*, *35*(6), 837–852, https://doi.org/10.1016/0042-6989(94)00185-O.

Mukherjee, T., Battifarano, M., Simoncini, C., & Osborne, L. C. (2015). Shared sensory estimates for human motion perception and pursuit eye movements. *The Journal of Neuroscience*, *35*(22), 8515–8530, https://doi.org/10.1523/JNEUROSCI.4320-14.2015.

Pastukhov, A. (2011). edfImport (Version 1.0.4): Matlab interface to Eyelink edf files. *Open Science Framework*. https://doi.org/10.17605/OSF.IO/FXUMN.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*(4), 437–442.

Rasche, C., & Gegenfurtner, K. R. (2009). Precision of speed discrimination and smooth pursuit eye movements. *Vision Research*, *49*(5), 514–523, https://doi.org/10.1016/j.visres.2008.12.003.

Schütz, A. C., Braun, D. I., & Gegenfurtner, K. R. (2011). Eye movements and perception: A selective review. *Journal of Vision*, *11*(5):9, 1–30, https://doi.org/10.1167/11.5.9. [PubMed] [Article]

Shapiro, A., Lu, Z.-L., Huang, C.-B., Knight, E., & Ennis, R. (2010). Transitions between central and peripheral vision create spatial/temporal distortions: A hypothesis concerning the perceived break of the curveball. *PLoS One*, *5*(10), e13296, https://doi.org/10.1371/journal.pone.0013296.

Smeets, J. B. J., & Hooge, I. T. C. (2003). Nature of variability in saccades. *Journal of Neurophysiology*, *90*(1), 12–20, https://doi.org/10.1152/jn.01075.2002.

Spering, M., & Gegenfurtner, K. R. (2007). Contrast and assimilation in motion perception and smooth pursuit eye movements. *Journal of Neurophysiology*, *98*(3), 1355–1363, https://doi.org/10.1152/jn.00476.2007.

Spering, M., Kerzel, D., Braun, D. I., Hawken, M. J., & Gegenfurtner, K. R. (2005). Effects of contrast on smooth pursuit eye movements. *Journal of Vision*, *5*(5):6, 455–465, https://doi.org/10:1167/5.5.6. [PubMed] [Article]

Spering, M., & Montagnini, A. (2011). Do we track what we see? Common versus independent processing for motion perception and smooth pursuit eye movements: A review. *Vision Research*, *51*(8), 836–852, https://doi.org/10.1016/j.visres.2010.10.017.

Stone, L. S., & Krauzlis, R. J. (2003). Shared motion signals for human perceptual decisions and oculomotor actions. *Journal of Vision*, *3*(11):7, 725–736, https://doi.org/10:1167/3.11.7. [PubMed] [Article]

Suehiro, K., Miura, K., Kodaka, Y., Inoue, Y., Takemura, A., & Kawano, K. (1999). Effects of smooth pursuit eye movement on ocular responses to sudden background motion in humans. *Neuroscience Research*, *35*(4), 329–338, https://doi.org/10.1016/S0168-0102(99)00098-X.

Tavassoli, A., & Ringach, D. L. (2010). When your eyes see more than you do. *Current Biology*, *20*(3), R93–R94, https://doi.org/10.1016/j.cub.2009.11.048.

Terao, M., & Murakami, I. (2011). Compensation for equiluminant color motion during smooth pursuit eye movement. *Journal of Vision*, *11*(6):12, 1–12, https://doi.org/10.1167/11.6.12. [PubMed] [Article]

Thompson, P. (1982). Perceived rate of movement depends on contrast. *Vision Research*, *22*(3), 377–380.

Wickham, H. (2009). *ggplot2 - Elegant graphics for data analysis*. New York, NY: Springer-Verlag. Retrieved from http://www.springer.com/us/book/9780387981406

Wilmer, J. B., & Nakayama, K. (2007). Two distinct visual motion mechanisms for smooth pursuit: Evidence from individual differences. *Neuron*, *54*(6), 987–1000, https://doi.org/10.1016/j.neuron.2007.06.007.

Zhang, J., Yeh, S. L., & De Valois, K. K. (1993). Motion contrast and motion integration. *Vision Research*, *33*(18), 2721–2732.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Springer.