

# ACHIEVING VISUAL STABILITY DURING SMOOTH PURSUIT EYE MOVEMENTS: DIRECTIONAL AND CONFIDENCE JUDGEMENTS FAVOR A RECALIBRATION MODEL

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## ABSTRACT

During smooth pursuit eye movements, the visual system is faced with the task of telling apart reafferent retinal motion from motion in the world. While an efference copy signal can be used to predict the amount of reafference to subtract from the image, an image-based adaptive mechanism can ensure the continued accuracy of this computation. Indeed, repeatedly exposing observers to background motion with a fixed direction relative to that of the target that is pursued leads to a shift in their point of subjective stationarity (PSS). We asked whether the effect of exposure reflects adaptation to motion contingent on pursuit direction, recalibration of a reference signal or both. A *recalibration* account predicts a shift in reference signal (i.e. predicted reafference), resulting in a shift of PSS, but no change in sensitivity. Results show that both directional judgements and confidence judgements about them favor a recalibration account, whereby there is an adaptive shift in the reference signal caused by the prevailing retinal motion during pursuit. We also found that the recalibration effect is specific to the exposed visual hemifield.

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<sup>1</sup> Why would anyone bother with a post-print? The typeset version was taken down from ResearchGate.net with 200'000 others after a mass request from Elsevier: <https://www.researchgate.net/blog/post/a-note-on-recent-content-takedowns>.

## INTRODUCTION

Perceptual motion constancy, or more generally visual stability, is among the most fundamental tasks the visual system must solve. Whenever motion is sensed on the retina there is an ambiguity regarding what events caused it: does motion happen in the world (objective motion) or is it the consequence of our own movements? This is an acute problem because our eyes are frequently moving within the orbit and so is the body. When we pursue a moving object, its motion on the retina is nulled. When both the eyes and the target move, objective motion does not equal motion on the retina, but it can be retrieved by relating extraretinal information about eye movement velocity and the retinal motion of the target. However, the visual system is faced with the issue that eye velocity information is inaccurate and imprecise (Bridgeman et al., 1994; Freeman et al., 2010). It is therefore likely that additional mechanisms are normally used to achieve motion constancy across eye movements (Haarmeier et al., 2001; Terao & Nishida, 2020). Here we focus on image-based recalibration mechanisms which may help to improve accuracy, and which may be based on a prediction error.

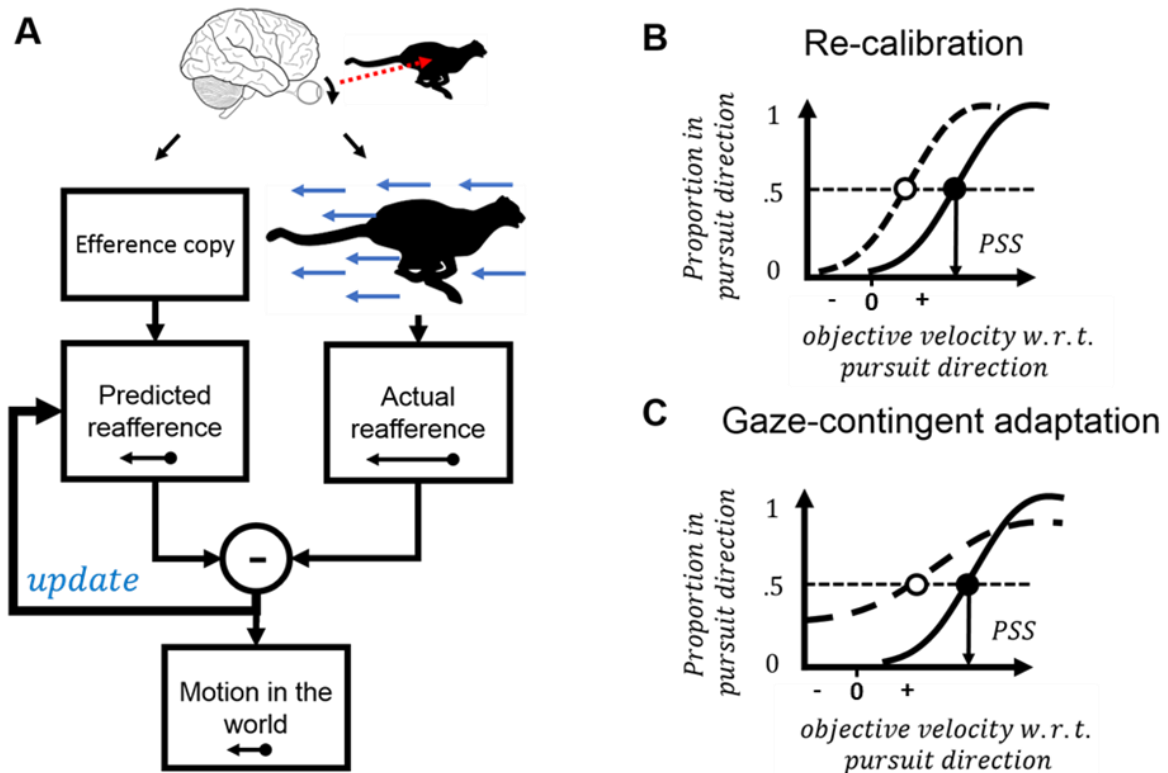
For a long time, extraretinal information—obtained from proprioception or from an efferent copy of the signal sent to eye muscles—was thought to be the primary source of information for achieving motion and space constancy across eye movements (Bridgeman, 2007; Bridgeman et al., 1994). However, the inaccuracy of the signal may be demonstrated by the Aubert-Fleischl and Filehne effects (Aubert, 1886; Filehne, 1922; Honda, 1990; Mack & Herman, 1978; von Fleischl, 1882), where background motion is underestimated during pursuit compared to fixation (Aubert-Fleischl) and where background motion is seen during pursuit while the background is static (Filehne). A more general and tractable solution to derive objective motion is to judge motion relative to a fixed world-reference. The importance of relative motion cues for perception has been demonstrated many times (Anstis & Casco, 2006; Duncker, 1929; Dürsteler, 2014; Spering & Gegenfurtner, 2007). Unlike extraretinal signals, static references can also be used to retrieve objective motion despite body translation. Evidence of the use of static references in image stabilization comes from the literature on miniature eye movements (drifts and microsaccades). Eye movements induce a specific regular pattern of motion in the image (i.e. optic flow). By picking up those regularities we are able to discount this self-induced component from the image (Murakami & Cavanagh, 1998, 2001). The efficacy of this mechanism is demonstrated by reduced motion discrimination thresholds in the presence of a visual reference during fixation (Raghunandan et al., 2008). The role of static references in specifying objective movement is also shown by the perceived movement of an afterimage (Pelz & Hayhoe, 1995). Observers misattribute movement—induced by eye micromovements—to the afterimage because it moves relative to the surrounding room features (see also Poletti et al., 2010). Finally, static

references may also be important in achieving position constancy across saccades (Deubel et al., 2010).

More evidence for the crucial role of image-based mechanisms for extracting objective motion during pursuit comes from the study of Haarmeier et al. (2001), showing that repeated exposure to background motion with the same direction relative to the pursuit direction leads to a shift in the point of subjective stationarity (PSS). This exposure effect could be thought of as mimicking a visual system that would misestimate the speed of pursuit and therefore will misattribute reafferent motion to motion of the background in world-coordinates. A stationarity prior indicates that the background does not tend to move in the world during pursuit and therefore any motion sensed tends to be entirely reafferent. It is therefore adaptive for the visual system to update predictions about reafference when being exposed to a background that is moving in the world. A model that takes into account a stationarity prior and assuming an ideal observer weighting information by its reliability could account for Aubert-Fleischl and Filehne illusions (Freeman et al., 2010). To put more clearly, if the speed of pursuit is underestimated, the amount of reafference is underestimated and an object that is static in the world should be seen as objectively moving in a direction that is opposite to that of pursuit, since too little reafferent motion is subtracted from the retinal image. Analogous to what is shown in the field of motor learning (e.g. Wolpert et al., 2011) it appears that the visual system gradually updates its prediction of reafferent motion based on a prediction error, that is, the mismatch between expected and observed reafference, allowing to maintain accuracy in extracting objective motion. Early arguments for plastic internal representations come from von Holst and Mittelstaedt (1950), specifying the need for them to be updated in response to changes in the environment. Later, Bell (1981) discovered modifiable efferent copy signals in the passive electrosensory system of mormyrid fish (see Fukutomi & Carlson, 2020, their “Corollary discharge is used to generate predictions and memories” section).

Here, we test two main predictions of how the visual system updates reafferent motion estimates. We sought to tell apart a recalibration account (Haarmeier et al., 2001) from a gaze-contingent adaptation account (e.g. Nishida et al., 2003; Parwaga et al., 2016) of the effect of exposure to background motion on objective motion judgements. Figure 1 illustrates how objective motion can be extracted by subtracting predicted reafference (as generated based on an efference copy signal) from retinal motion, while Figure 1B-C contrasts two alternative ways in which exposure to background motion could affect perceptual judgements about the direction of background motion in world-coordinates. In our view, a recalibration account (Figure 1B), as proposed by Haarmeier et al. (2001), states that the effect of exposure is to shift predicted reafference, so that it comes closer into alignment with the background motion to which the observer is exposed to. In practical terms, there will be a shift of the PSS, but no effect on sensitivity to motion, that is, the ability to discriminate between quantities of background motion. A gaze-contingent adaptation account, (Figure 1C), would state that there is motion adaptation contingent upon the direction of pursuit. Since there are motion

detectors in the brain that encode motion relative to pursuit direction (e.g. Chukoskie & Movshon, 2009b; Lee et al., 2011), we may also hypothesise as well the existence of motion adaptation contingent upon the direction of pursuit. Evidence for gaze-contingent adaptation can be found in saccade studies, where motion and tilt aftereffects specific to saccade direction can be observed (Mayhew, 1973; Nishida et al., 2003; Parwaga et al., 2016). Adaptation can be seen as the way the visual system encodes the context of a visual stimulus, as there is rapid adaptation of neural responses, such as depending on the preceding stimulus speed and direction (Kohn, 2007). Motion adaptation greatly reduces contrast sensitivity of neurons tuned to the adapted stimulus in macaque MT (Kohn & Movshon, 2003). It is not clear how changes in neural responses translate onto perceptual judgements. However, there is a clear reduction in perceived speed and to a lesser extent direction discrimination when a dot pattern differing in speed or direction is presented contiguously in time compared to when it is presented a second apart, suggesting an effect of rapid adaptation on motion discrimination (Mateeff et al., 2000; Schlack et al., 2007). In our case, a gaze-contingent adaptation account would predict a change in the slope of the psychometric function. Reduced discriminability may as well lead to a shift in PSS, as a weaker sensory signal will shift the weight of evidence towards prior evidence of stationarity (Freeman et al., 2010; Weiss et al., 2002). In summary (Figure 1B-C), the recalibration account would predict that the sensory processing of reafference is intact, resulting in a horizontal shift of the psychometric function. In the adaptation account, motion discrimination is reduced, resulting in a shallower slope in discriminating background motion direction.



**Figure 1.** Reafference principle and model predictions. Panel A illustrates a model of how objective motion (motion in the world) can be retrieved when the observer tracks a moving object (e.g. the panther) with the eyes. Retinal motion (blue vectors) emanating from the background (the part of the image surrounding the tracked object which would normally contain environment features that are stationary in the world) here is purely reafferent (caused by the eye movement). The brain can predict the amount of reafferent motion from extra-retinal signals such as an efference copy of the oculomotor command. The subtraction of the actual and predicted reafference yields a prediction error that can be used to extract the amount of objective motion in the image and be used as a teaching signal to update future predictions under the assumption that background features are static in the world. Panels B and C contrast two predictions regarding how directional judgements change after exposure to background motion opposite to the pursuit direction. The x-axis (objective velocity with respect to [w.r.t.] pursuit direction) shows the objective velocity of background motion with a sign that depends on the pursuit direction (a positive sign means the motion is in the direction of pursuit) and the y-axis the proportion of responses in the pursuit direction. Under regular conditions (solid lines), we expect the point of subjective stationarity (PSS) to be positive, since stationary objects are perceived to move against the pursuit direction in the Filehne illusion (Filehne, 1922). Panel B illustrates a recalibration process in response to exposure of background motion opposite to the pursuit direction, by which the PSS is shifted to reduce the prediction error (dashed line), whereas the discriminability of motion around the PSS remains the same to the previous state (solid line). Panel C illustrates the hypothetical effect of gaze-contingent adaptation on objective motion judgements. In that case motion detectors tuned to reafferent retinal motion relative to the pursuit direction reduce their response, resulting in reduced discriminability of dots velocity, as indicated by a shallower slope at the PSS (dashed line), compared to an unaffected state (solid line). The PSS might also be shifted, due to giving relatively more weight to prior information regarding the likelihood of stationarity (the stationarity prior).

Another way to explore the effect of exposure on the updating of objective motion estimates is to look at the spatial selectivity of the effect. Neurons higher in the visual hierarchy tend to integrate motion information over larger receptive fields (Adelson & Bergen, 1985; Adelson & Movshon, 1982; S. J. Anderson et al., 1991, 1991; Stephen J. Anderson & Burr, 1985, 1989). On top of this hierarchy, MST neurons (Tanaka et al., 1993) are well suited to analyze the reafferent optic flow patterns induced by eye movements, as they cover the entire visual field. A recalibration mechanism compensating for prediction errors should ideally operate at a global scale, given that eye movements produce a global change in the retinal image (Souto et al., 2019). Therefore prediction errors observed at different locations in the visual field could lead to a global updated estimate of the reafference signal.

Lastly, it remains possible that the shifts in PSS that were observed by Haarmeier et al. (2001) are due to a gaze-contingent response bias. For instance, exposure could increase the proportion of responses opposite to the direction of the exposed motion, which would result in a similar shift of psychometric functions. To rule out this possibility we used a novel way of disentangling response bias from a sensory change by asking for confidence in addition to directional judgements. Gallagher et al. (2019) showed that high and low confidence judgements can be fitted by a psychometric function, from which a point of minimal confidence can be extracted and which corresponds to a point

of subjective equivalence in the absence of a response bias. Therefore, single-interval forced-choice confidence judgements would allow to rule out or confirm a response bias. Concretely, the point of minimal confidence and the PSS should correspond to the same objective motion estimate if the PSS represents the point at which the observer is maximally uncertain about the direction of the stimulus (i.e. sensory bias) and is not the result of a response bias (whether strategic or not).

## METHODS

### PARTICIPANTS

Seventeen participants (22-31 yo) took part in Experiment 1, six were excluded from further analysis as they did not show regular psychometric functions in the control condition (the contrast of the stimulus was very low in that experiment); in the remainder participants the goodness-of-fit of the psychometric functions was assessed calculating the Deviance or log-likelihood ratio between the likelihood of the saturated model (i.e. with no residual errors between empirical data and model predictions) and the likelihood of the best-fitting model or  $D = 2 \cdot \log \left( \frac{\text{saturated model likelihood}}{\text{best-fitting model likelihood}} \right)$  (Wichmann & Hill, 2001). We then compared the Deviance against the Chi-square distribution ( $p$ -values  $> .05$  are considered a good fit, see Appendix A, Figures A1 and A2). For Experiment 1, the averaged Deviance was 51 (44-67 [min-max]),  $p > .05$ . Twelve participants took part in Experiment 2 (21-39 yo). Two quit the study before the end and one was excluded for not showing regular psychometric functions. Deviance was on average 6.29 (0.33-26.18, [min-max]),  $p > .05$ , except for participants 1, 3 and 7 in the same visual field exposure condition (Appendix A, see Figure A2). Participants were undergraduate students in Experiment 1 and 2 except for two of the authors (DS, RL) and a member of staff in Experiment 2. Participants (except authors) were given course credits for participation, were paid 8 Euros per hour in Giessen and £8.2 per hour in Leicester. Each of them gave his/her informed consent to participate. We abided by the principles of the Declaration of Helsinki (1964). Ethical approval was granted by the local ethics committee of the Department of Psychology at the University of Giessen (Experiment 1, LEK 2017-0029) and the School of Psychology Ethics Committee from the University of Leicester (Experiment 2, 21667-ds572).

### MATERIALS AND VISUAL STIMULATION

Eye movements were recorded with Eyelink 1000 (Experiment 1, Giessen) and II (Experiment 2, Leicester) eye trackers (SR, Osgoode, Canada). Stimuli were programmed by using the Psychophysics toolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) in Matlab (Mathworks, Natick, US) and displayed on a ViewPixx (Saint-Bruno, Canada) monitor, 120 Hz, 1920 x 1080 pixels (Experiment 1) and an OLED 55 inch (OLED55B8SLC, LG, Seoul, South Korea) monitor, 60 Hz,

1920 x 1080 pixels (Experiment 2). Using a chin- and front-rest, the participants' viewing distance was 48 cm in Experiment 1 and 110 cm in Experiment 2.

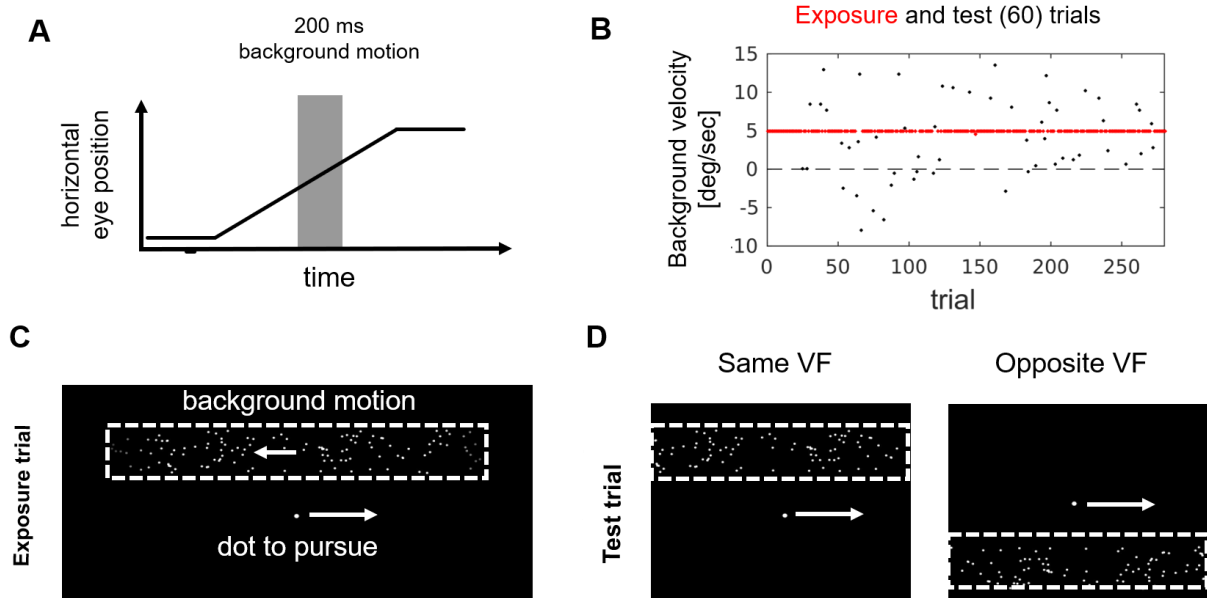
We reduced to the minimum light outside from that emitted by the screen to remove the availability of any external reference which could have been used to estimate motion in the world, such as coming from the screen edges. In Experiment 1, we achieved this by overlaying three .9 neutral density filters (each filter let 10% of light through over all visible wavelengths) in front of the screen. This means that the luminance of the stimulus (using the full brightness of the screen, 228 cd/m<sup>2</sup>) was only 0.23 cd/m<sup>2</sup>. We avoided dark adaptation by programmatically switching on a bright lamp every five minutes.

In Experiment 2, the use of an OLED screen allowed us to use a bright stimulus, of 100 cd/m<sup>2</sup> (we found out that the maximal brightness of 250 cd/m<sup>2</sup> was uncomfortable), because we did not have to filter light coming from the screen, since no light is emitted from black pixels in OLED displays and there was no screen edge on which light could be scattered. Measurements on two other OLED screen models showed good properties for vision research, such as a fast and symmetric on and off temporal response (Cooper et al., 2013).

## PROCEDURE

### *Experiment 1: Effect of exposure and visual field*

The procedure is illustrated in Figure 2A-D. In all trials observers had to track a dot moving horizontally across the centre of the screen (7.6 deg/sec speed, 0.4 deg size), as shown in Figure 2A. The dot started moving 10 deg away from the centre (left/right side of the screen) and ended its movement 10 deg on the opposite side (right/left side of the screen). The dot movement direction (leftward/rightward) was randomized. In the middle of the trajectory, meaning 1.3 s after the motion started, a cloud of randomly located dots was displayed for 200 ms through a horizontal aperture (Figure 2C) in the periphery (4 x 30 deg, +/-6 deg eccentricity). Their density was of one dot per deg and each dot (0.2 deg diameter) moved coherently for 200 msec. We removed accretion and deletion speed as a source of information by tapering the contrast of dots as they approached the horizontal borders of the display area. We did so by modulating the contrast by a half-Gaussian with a 2 deg sigma, starting 5 deg from the borders. Note that the target trajectory and background motion was perfectly predictable. However, the alternative (random presentation along the trajectory) would have complicated matters by making the dual task more difficult, increasing the likelihood that observers would miss background information by having them attend to the background along the whole pursuit trajectory and introducing effects of retinal eccentricity on the perceptual and pursuit measures.



**Figure 2.** Experimental procedure. A. Pursuit target trajectory. The gray area shows the 200 ms interval over which a cloud of dots in the background was displayed. B. In an exposure trial, the background was moving with a velocity (here 5 deg/sec), whereas in a test trial, different background motion velocities are shown to map the psychometric function and find the point of subjective stationarity (PSS). C. Screen copy showing the dimensions of the dot-cloud and the tapering off at the edges of the dot contrast with horizontal eccentricity. D. In test trials, the dot-cloud was located either in the same or opposite visual field (VF) relative to the exposure trials.

To test the effect of exposure on objective motion estimates we compared a control and exposure condition in separate blocks of trials. In the control condition, run in one session, there were only test trials. In those trials, the observers' task was to report the direction of background motion by using the left/right arrows of the keyboard. The background dots' velocity was varied by using an adaptive maximum-likelihood procedure as implemented by the UML Matlab toolbox (Shen et al., 2015), meaning that the most informative dot velocity was picked on every trial to constrain an estimate of the observers' PSS. Visual field (upper or lower) was randomized across trials, with 60 trials per visual field to test the visual field specificity of the exposure effect.

In the exposure condition there was a majority of exposure trials during which the observer only had to pursue the central dot. In exposure trials, subjects simply pursued the central dot and experienced background motion with a fixed velocity (5 deg/sec or -5 deg/sec) within a session. No perceptual judgment was probed in these trials. The visual field exposed was always the upper visual field (VF). Background velocity henceforth is expressed with respect to the pursuit direction, with positive and negative values indicating motion in the direction of pursuit or opposite to it respectively. In each session there were 280 trials in total. 60 test trials (21% of the total) were interleaved randomly with exposure trials from trial 20 onward. There were two exposure sessions, meaning again 60 trials



per visual field. Figure 2B shows background dots velocity on every trial in one exposure session, with exposure to 5 deg/sec. During exposure trials, the background dots appeared either in the same or the opposite VF relative to the field in the exposure trials (Figure 2D).

### *Experiment 2: Directional and confidence judgements*

In a second experiment, we asked observers to provide directional responses and confidence judgements. The goal of that experiment was to be able to tell apart two possible models of how exposure affects objective motion judgements (see Figure 1). Because we wanted to compare psychometric function slopes in addition to the PSS, we used the method of constant stimuli with many more test trials (160-240) per function.

The procedure was generally the same as that used in Experiment 1. During the exposure condition, we changed the proportion of test (80 trials, 31%) and exposure trials (180 trials, 69%) per session, to maximize the number of test trials (in keeping with Haarmeier et al. 2001). The pursuit dot (0.4 deg) moved at 10 deg/sec over a 20 deg range. The same background motion eccentricities were used, while the display area (9 x 30 deg at 6 deg eccentricity) and dot size (0.2 deg, 1 dot per deg density) were different, as we could increase stimulation area, thereby potentially maximizing effects, with the larger OLED screen.

In this experiment we balanced the exposed visual field across participants. Five participants (of the remaining sample after exclusion) were tested with exposure in the upper VF. In the remaining four the lower VF was exposed. As in Experiment 1, in the exposure condition, the test background motion was located either in the same or opposite VF relative to the exposure trials. We used only one exposure velocity of -5 deg/sec, as this generated a robust effect in Experiment 1. We reasoned that the reference needs to be far from the PSS before exposure to maximize effects. According to Experiment 1 the PSS lies at around 5 deg/sec in the direction of pursuit (although with a slower pursuit speed), meaning that there is a 10 deg/sec difference between what is considered as static and the motion experience. However, we also reasoned that a hypothetical effect of recalibration would be weaker if the speed is too far from the expected reafference (and discounted as an external event; see Souto et al. 2016), stopping us from venturing beyond -5 deg/sec exposure.

Using the method of constant stimuli to map psychometric functions, on every test trial background test velocities of -5, -4, 0, 3, 6, 10, 15, and 20 deg/sec were picked randomly. Fits were based on 20-30 trials per test velocity. An important difference with Experiment 1 is that, on test trials observers were asked to report binary judgements of confidence about their directional responses by using the keyboard up and down keys, to signify “high” or “low” confidence. Therefore, observers first gave a directional response (left/right) and then a confidence judgement. To avoid confusion there was always a text prompt being displayed, specifying the type of response required (directional or

confidence response). This method of recording confidence judgements has been introduced by Gallagher et al. (2019) as a general method of ruling out of response biases. To derive a good estimate of the slope and PSS, we ran 2-3 control sessions (only test trials) followed by 2-5 exposure sessions (reference + test).

## DATA ANALYSIS

A maximum-likelihood procedure was used to fit psychometric functions to the proportion of directional responses in the pursuit direction. The equation used for these functions was the following (Wichmann & Hill, 2001):

$$\Psi(x; \alpha; \beta; \gamma; \lambda) = \gamma + \frac{(1-\gamma-\lambda)}{2} \left[ 1 + \operatorname{erf} \left( \frac{x-\alpha}{\beta\sqrt{2}} \right) \right] \quad (1)$$

In Equation 1,  $\gamma$  is the guess rate and  $\lambda$  is the lapse rate. The expression in square brackets stands for the cumulative Gaussian function, with  $x$  being the background dots velocity,  $\alpha$  the PSS and  $\beta$  the standard deviation. The parameters being fit through the maximum-likelihood procedure were  $\alpha$ ,  $\beta$  and  $\lambda$ , with  $\gamma = \lambda$ . The Matlab (Mathworks, Natick, US) function `fminsearchbnd` (John D’Errico, 2020) was used to find the best-fitting psychometric functions, restricting the parameter searching space ( $[-15, 15]$  for  $\alpha$ ,  $[1.5, \infty]$  for  $\beta$ , and  $[0, 0.4]$  for  $\lambda$ ).

For the confidence judgements, we fitted the proportion of high confidence judgements with the following inverted Gaussian function using the non-linear least squares method:

$$C(x) = 1 - \left( a e^{-\frac{(x-\mu)^2}{2\sigma^2}} \right) \quad (2)$$

In Equation 2,  $x$  is the drifting speed,  $a$  modulates the minimum confidence judgment,  $\mu$  is the position (i.e. speed) of the minimum, and  $\sigma$  is the standard deviation. The “Curve Fitting” toolbox from Matlab was used to perform the fittings.

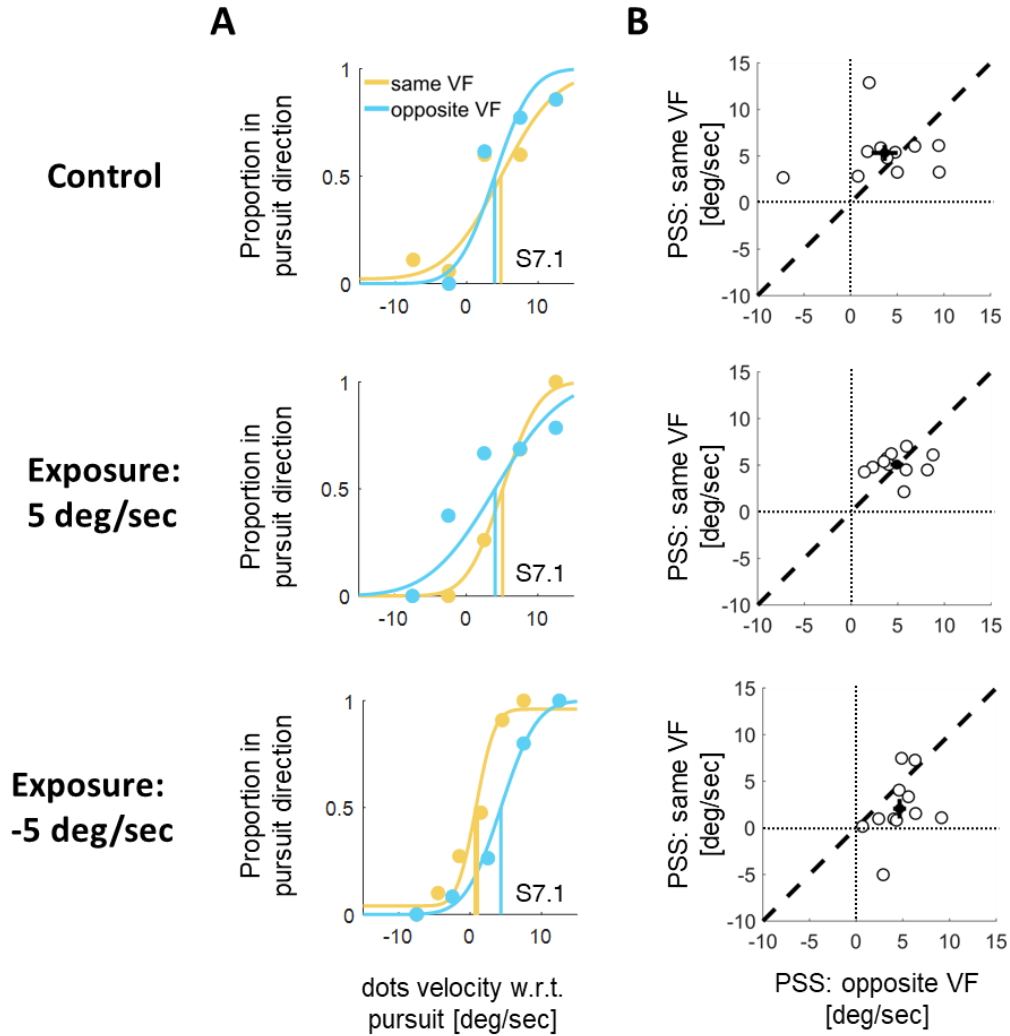
Gallagher et al. (2019) showed how the proportion “high” confidence can be fit by this type of function, allowing one to extract the minimal confidence point. Unless there is a response bias, confidence should reflect sensory uncertainty. Therefore, the point of minimal confidence should align with the velocity PSS, provided that the responses are bias-free.

The analysis of eye movements was an afterthought. We initially intended to use the eyetracking only for the experimenter to ensure participants were doing the pursuit task by using the eyetracker’s live feed. Therefore we included in the experiment participants whose eye movements could not be reliably recorded, typically due to wearing glasses or lenses. We analyzed the eye movement data of 7 participants from Experiment 1 and 8 participants from Experiment 2; including

those participants for which valid eye movement recordings could be obtained in all conditions of interest. We identified saccades by using the Eyelink (1000/II) parser, based on an acceleration ( $>4,000$  deg/sec<sup>2</sup>) and a velocity criterion ( $>22$  deg/sec). Trials in which blinks or saccades occurred during the background motion were discarded from the eye movement analysis (not from the psychophysical analysis), which amounted to 8% of trials on average per individual (0-30%, SD = 12%) in Experiment 1, and 17% (4-42%, SD=15%) in Experiment 2, to provide an accurate measure of the pursuit response to the background motion, as it would be indicative of an influence of pursuit accuracy (as indicated by pursuit gain, eye velocity / target velocity) on our perceptual measures. We obtained pursuit velocity by using a two-point central differentiation method, with a 20-ms step (Bahill & McDonald, 1983).

## RESULTS

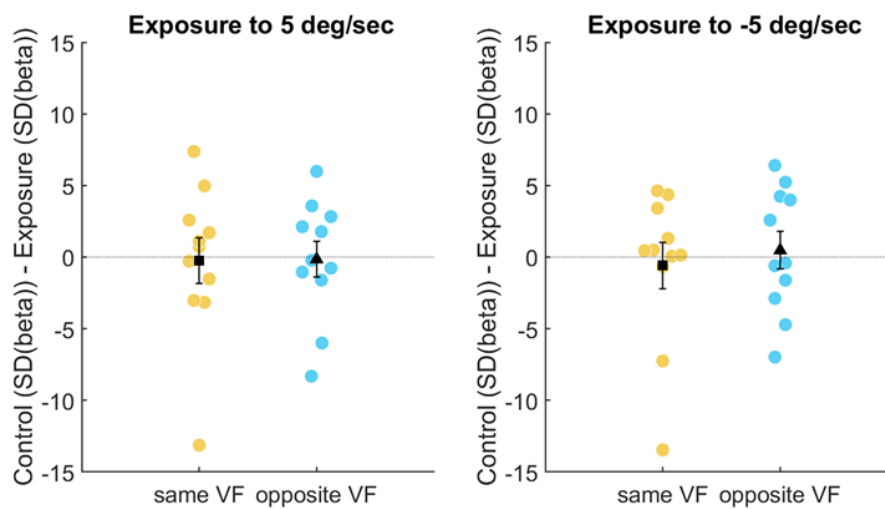
In the first experiment we adapted Haarmeier et al.'s (2001) paradigm to test whether exposure to background motion during pursuit affects objective motion within the exposed VF or globally across upper and lower VFs. Figure 3A shows psychometric functions from which the PSS can be extracted, in control (no exposure) and exposure conditions, in a representative participant (S7.1). In the control condition, the PSS is about 5 deg/sec in the direction of pursuit, consistent with the classical Filehne effect (Filehne, 1922). After being exposed to 5 deg/sec in the direction of pursuit (in the upper VF), the PSS remained unchanged, whether the test was presented in the same VF or the opposite VF. In contrast, after exposure to -5 deg/sec the PSS shifted by about 5 deg/sec towards 0 when judging motion in the same VF, but not in the opposite VF. Figure 3B shows the individual PSS and group average in the control and exposure conditions. Again, the effect of exposure is only pronounced with the same VF and with exposure to -5 deg/sec background velocity. At the group level, a repeated-measures ANOVA (background velocity 2 x visual field 2) on the shift of PSS compared to the respective control condition, confirmed a main effect of exposure,  $F(1,10)=8.399$ ,  $p < .02$ , which could be accounted for by the PSS being shifted by a greater amount (-1.16 deg/sec) after exposure to -5 deg/sec than after exposure to 5 deg/sec (0.49 deg/sec), and an interaction between background velocity and visual field,  $F(1,10)=5.027$ ,  $p < .05$ . The interaction could be explained by exposure to 5 deg/sec having a more similar PSS compared to control, either for opposite (1.22 deg/sec) and same VF (-.24 deg/sec),  $t(10)=0.315$ ,  $p=.759$ , whereas exposure to -5 deg/sec shifted the PSS in the direction of the exposed motion in a greater amount in the same VF (-3.32 deg/sec) but not the opposite VF condition (+0.98 deg/sec),  $t(10)=2.570$ ,  $p = .028$ .



**Figure 3.** Experiment 1 data. A. Example psychometric functions for one participant in the control (upper panel) and exposure conditions where observers were exposed to 5 deg/sec (middle-panel) and -5 deg/sec background motion (lower panel) relative to the pursuit direction. The x-axis represents dots velocity with respect to (w.r.t.) the pursuit direction, with positive values indicating dots motion is in the direction of pursuit, negative values that they move opposite to pursuit. Each dot represents binned proportion responses only for visualization. The vertical lines indicate the PSS, i.e. the point at which there is an equal proportion of responses in either direction. We refer to the same VF or opposite VF condition, depending on which visual field is exposed in the exposure conditions, i.e. the same VF condition in the control condition refers to the VF that was exposed in the other conditions (See Figure A.1, in Appendix A for the rest of individual subjects' psychometric function fits). B. Group data with every dot representing an individual's PSS in the control condition (upper panel) and exposure conditions with exposure to 5 deg/sec (middle panel) and -5 deg sec (lower panel). The group averages for each condition are shown as filled black dots, along with 95 confidence intervals.

We also compared the standard deviation of the fitted psychometric function (the slope can be calculated by taking the inverse of the standard deviation) in the control and exposure conditions, to test the hypothesis that exposure would affect the ability to discriminate speed in addition to shifting

the PSS. To do so, the difference was taken between data values in the control condition and the values in the exposure conditions (exposure to 5 deg/sec and -5 deg/sec), separately for the same VF (the upper VF in this experiment) and the opposite VF (the lower VF in this experiment). Figure 4 allows to compare the effect of exposure on sensitivity (standard deviation) compared to control with the same VF or opposite VF. Within the same VF, there is no significant difference between exposure to 5 deg/sec and control,  $t(10)=0.15$ ,  $p=.88$ ,  $BF_{10}=0.30$ , or with exposure to -5 deg/sec and control,  $t(10)=-0.32$ ,  $p=.76$ ,  $BF_{10}=0.31$ . There is 3 times more evidence in favor the null hypothesis (in both cases), stating there is no difference in discriminability after exposure.

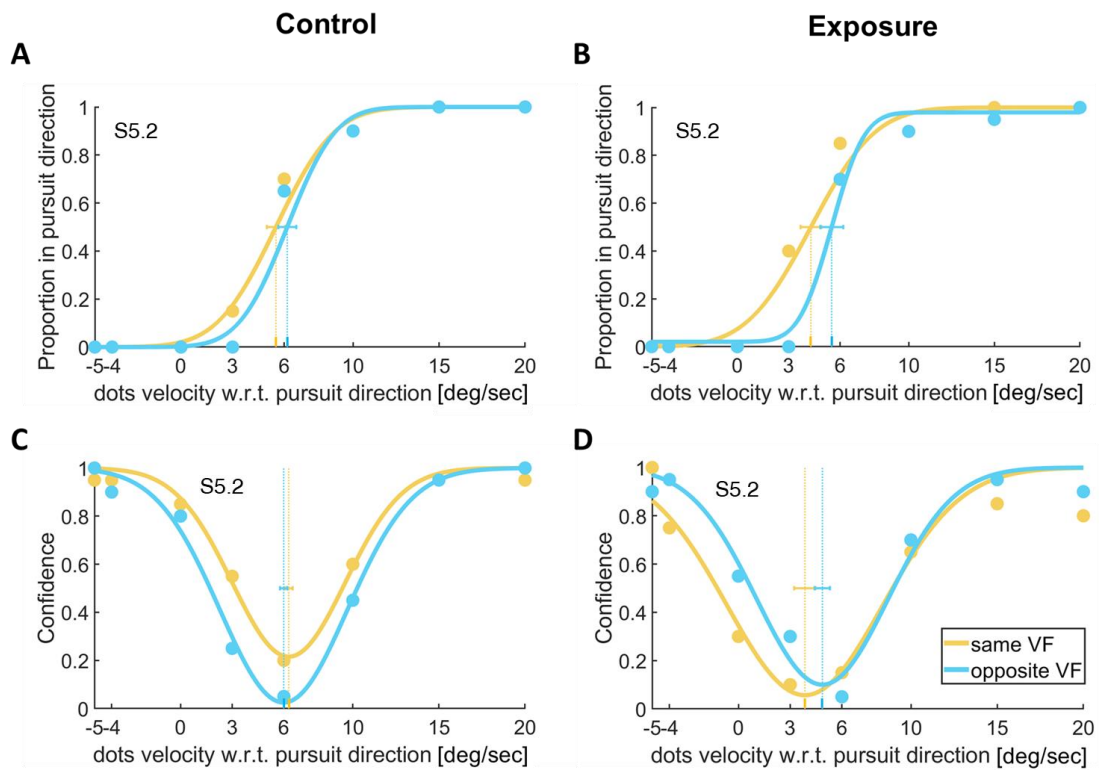


**Figure 4.** Exposure effect in Experiment 1. Effect of exposure on the standard deviation of the psychometric function fits, SD (beta), for directional judgements. Background dots during exposure trials in the exposure conditions had velocities of 5 deg/sec (left) and -5 deg/sec (right). Same/opposite VF is defined for test trials in the exposure condition relative to the exposed VF during exposure trials. Colored dots indicate values for individual subjects whereas black squares and triangles indicate the mean for same and opposite VF respectively. Error bars represent the standard error of the mean ( $\pm SEM$ ).

In the second experiment, we sought to derive robust psychometric fits to evaluate motion discriminability (i.e. obtain a robust estimates of the slope), the PSS and confidence judgements. Psychometric functions were this time based on 160-240 trials by using the method of constant stimuli, with 20-30 trials per stimulus level. Additionally, an inverted Gaussian function was fitted to the proportion of confidence judgements.

Figure 5 shows psychometric functions fitting directional and confidence judgements in one participant from Experiment 2 (S5.2). In Figure 5A, directional judgement fits are shown for the control condition where the subject reports directional judgements for moving dots in the upper and lower VFs. Figure 5B shows directional judgement fits in the exposure condition. This participant was exposed to background motion in the upper VF during exposure trials. Therefore, according to the

results from Experiment 1, if recalibration with a background drifting at  $-5$  deg/sec took place in this subject, a shift in the PSS for the test trials happening in the same VF should be observed. This is indeed the case, as can be seen as a shift in the orange marked PSS for same VF (Figure 5B) with respect to the corresponding control condition (Figure 5A), but not for the opposite VF marked blue. That is, the shift in the PSS relative to control is specific to the exposed VF. The same pattern is observed with the minimal confidence point in confidence judgements (Figure 5C-5D).

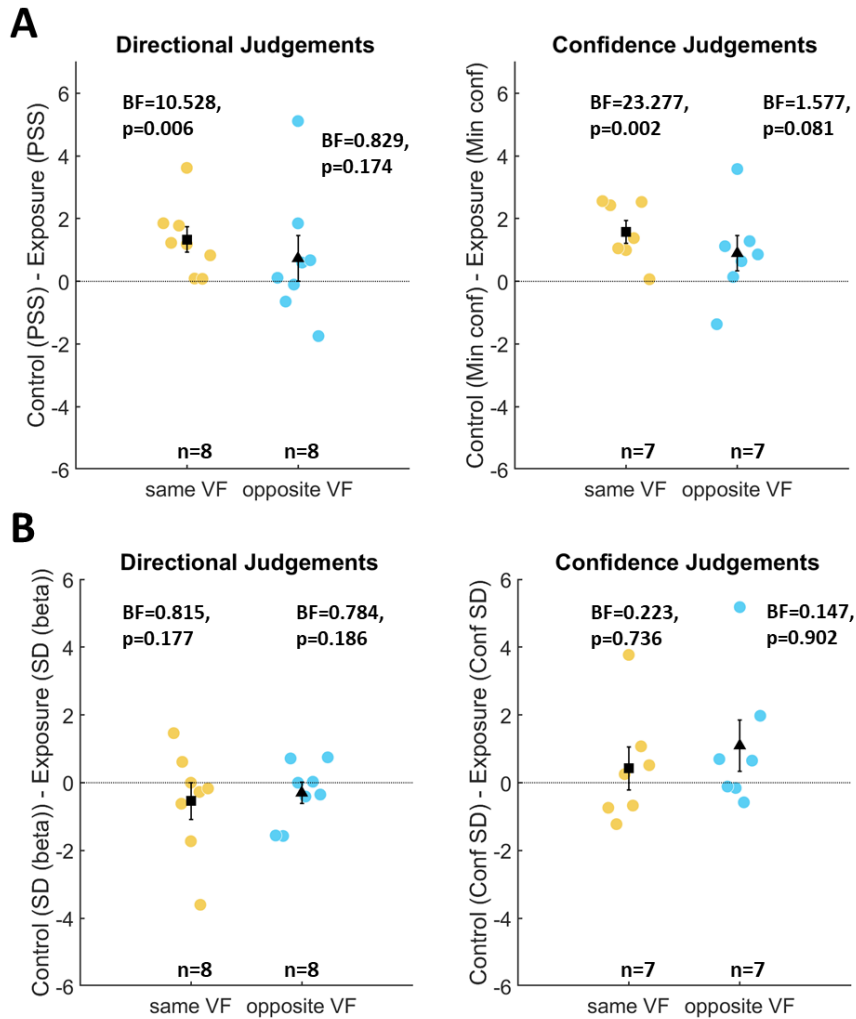


**Figure 5.** Results and fittings of a representative participant in Experiment 2. A-B: Proportion of directional judgements in the direction of pursuit as a function of background velocity (dots velocity with respect to [w.r.t.] pursuit direction) (See Figure A.2, in Appendix A for the rest of individual subjects' psychometric function fittings). A. Results for the control condition. B. Results for the exposure condition. The vertical lines indicate the PSS, i.e. the point at which there is an equal proportion of responses in either direction. C-D: Proportion of high confidence judgements as a function a background velocity. C. Results for the control condition. D. Results for the exposure condition. The vertical lines indicate the point of minimal confidence. We refer to same VF or opposite VF depending on which visual field is exposed in the exposure conditions, i.e. the same VF condition in the control condition refers to the VF that was exposed in the exposure condition. In all plots, horizontal lines designate the  $\pm$ SD of the PSS or point of minimal confidence. Non-parametric bootstrap was used to calculate the SD of the mean parameter (PSS) in the psychometric fits.

Figure 6 shows the group data from Experiment 2. In order to estimate the differences between the two conditions, the data values of the exposure condition have been subtracted from the values of the control condition by matching the visual field. This way we controlled for pre-existing effects of

visual field. For instance, if the upper visual field was exposed, the PSS for the same VF condition was subtracted from the matching control condition, that is the PSS corresponding to test trials with background motion in the upper VF.

Given the effect of exposure was already demonstrated in Experiment 1, the goal of Experiment 2 was to test whether this effect could be explained either under a re-calibration framework or a gaze-contingent adaptation one. We excluded participant S3.1 from this analysis, as they showed a strong shift (-3.18 deg/sec) opposite to everyone else, whether in Experiment 1 and 2, suggesting idiosyncratic behaviour. More precisely, the difference in PSS between the same VF exposure and control conditions was negative, contrary to what would be predicted by a recalibration or contingent adaptation account. We ran a repeated-measures t-test, showing a significant effect of the exposure condition on PSS. This effect of exposure on the PSS can be seen in Figure 6A (left panel). Replicating Experiment 1, the PSS was higher in the control condition than in the same VF of the exposure condition (PSS, same VF:  $t(8) = 3.303$ ,  $p = .006$ , PSS, opposite VF:  $t(8) = 1.005$ ,  $p = .174$ . Right-tailed repeated measures t-test). The same test run on the PSS was run on the point of minimal confidence (see Figure 6A, right panel); showing significantly higher values in the control condition than in the same VF of the exposure condition (Point of minimal confidence, same VF:  $t(7) = 4.333$ ,  $p = .002$ , Point of minimal confidence, opposite VF:  $t(7) = 1.594$ ,  $p = .081$ . Right-tailed repeated measures t-test). Thus, similarly to the PSS, confidence judgements only changed after exposure on the same VF. In addition, we used a Bayesian t-test to evaluate whether evidence favors the null or the alternative hypothesis. It shows evidence favorable for a shift in PSS (Figure 6A, left panel) and point of minimal confidence (Figure 6A, right panel) with no shifts in the standard deviation of the directional judgement fits (Figure 6B, left panel) or in the standard deviation of the confidence fits (Figure 6B, right panel) in the same VF condition. See the Bayes Factors, BF, and the associated p-values (t-tests are one-tailed for the directional judgements and confidence fits standard deviation, as a reduction in sensitivity by exposure would be expected). Evidence in favours a recalibration account rather than a gaze-contingent adaptation account.

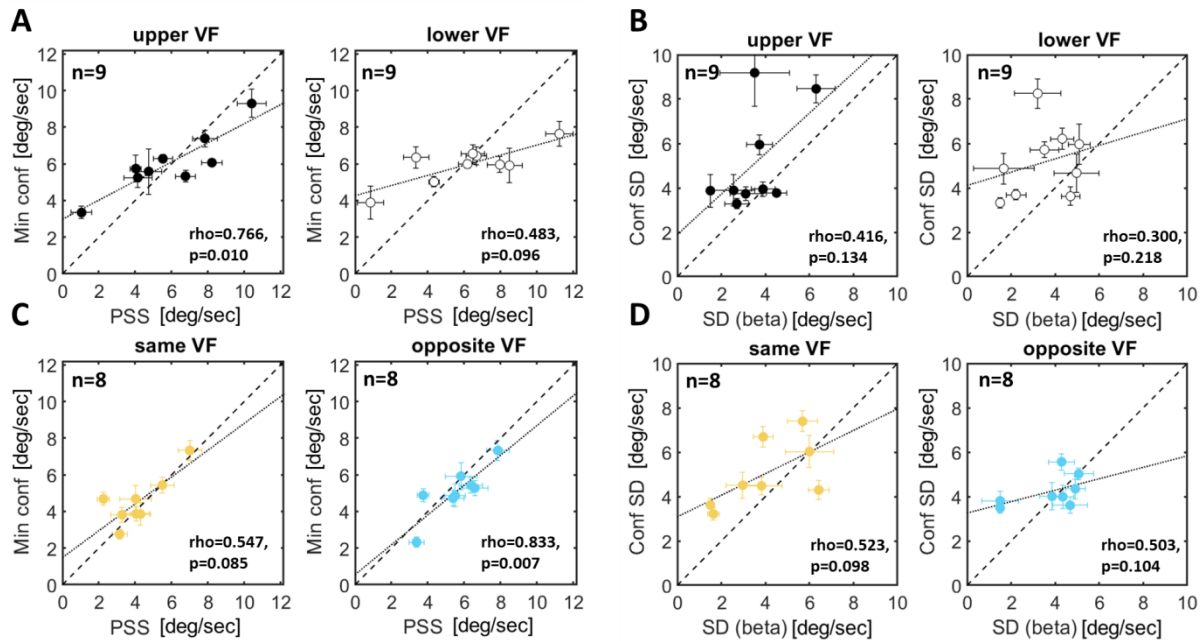


**Figure 6.** Exposure effect in Experiment 2. Panel A contrasts the effect of exposure on the PSS (left) and point of minimal confidence (right) for the same VF and opposite VF. Panel B contrasts the effect of exposure on the standard deviation of the psychometric function fits, SD (beta), for directional judgements (left) and the standard deviation of the corresponding confidence fits (right). Same/opposite VF is defined for test trials in the exposure condition relative to the exposed VF during exposure trials. Colored dots indicate values for individual subjects whereas black squares and triangles indicate the mean for same and opposite VF respectively. Error bars represent the standard error of the mean ( $\pm SEM$ ). In all panels, the Bayes factor, BF, from a Bayesian t-test and its associated p-value, p, is shown.

Another issue to resolve is whether directional and confidence judgements, taken together, favor a recalibration model. This implies checking if the shifts seen in the directional judgements can be predicted by confidence judgements. In this case, a shift in the point of minimal confidence should also be appreciated in a scenario where recalibration takes place. Importantly, significant differences between control and exposure PSS's for the same VF are paired with significant differences regarding the point of minimal confidence in the same VF condition. Conversely, no significant differences in PSS for the opposite VF are paired with no significant differences in this same condition for the point



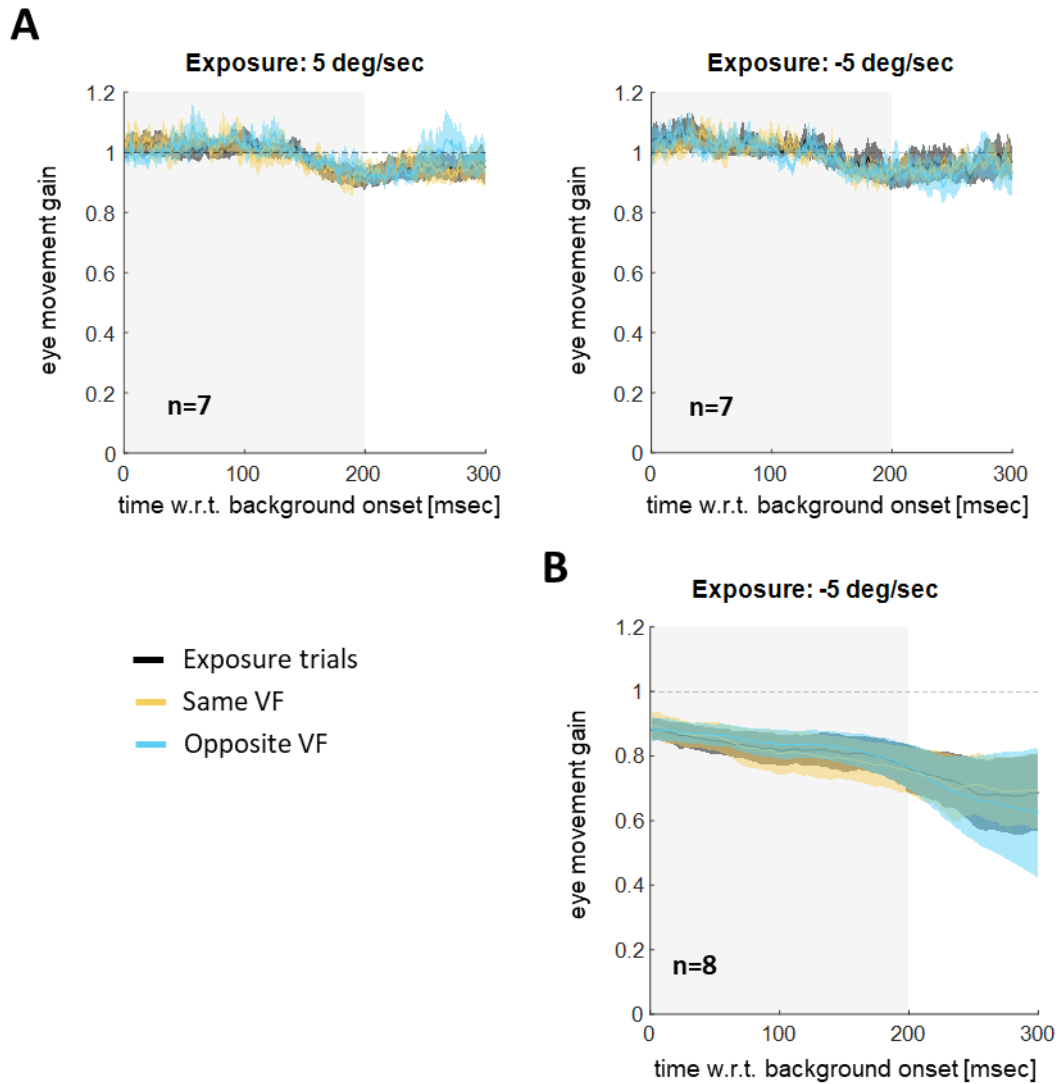
of minimal confidence. Additionally, Figures 7A and 7C show Spearman correlations between the point of minimal confidence and the PSS. Correlations ranged from .483 ( $p=.096$ ) to .833 ( $p=.007$ ), indicating that the point of minimal confidence can be a proxy for the PSS as suggested by similar effects of exposure on the PSS and point of minimal confidence in Figure 6A. The fact that the point of minimal confidence is correlated with the PSS suggests that the PSS reflects maximal uncertainty regarding sensory information and that the effect of exposure is not due to a response bias (Gallagher et al. 2019).



**Figure 7.** PSS against the point of minimal confidence in the control condition (Panel A) and the exposure condition (Panel C). Respectively for the control and exposure conditions, panels B and D show the standard deviation of the psychometric function fits (SD (beta)), i.e. an estimate of discriminability, against the standard deviation of the confidence function fits. Identity lines are shown as dashed black lines. One subject was excluded due to not showing regular inverted Gaussian fits in the same and opposite VF (graphs with  $n=8$ ). Horizontal and vertical lines designate the SD of the parameters on the x and y axes respectively. Non-parametric bootstrap was used to calculate the SD of the parameters in the psychometric fits.

Finally, Figures 7B and 7D show the Spearman correlations between the standard deviation derived from the directional judgement fits and the standard deviations of the inverted Gaussians fitted to the confidence data. These range from .300 ( $p=.218$ ) to .523 ( $p=.098$ ), showing a positive relationship between both (although not statistically significant). The standard deviation of the directional judgments fits and the standard deviation of the confidence judgement fits are both indicative of discriminability (e.g. due to sensory uncertainty); and those two measures should correlate perfectly if both judgements rely on the same sensory information.

It is of interest to test whether the differences in psychophysical results between conditions, both in Experiment 1 and 2, could be caused by changes in pursuit eye movements due to the exposure to background motion. Past studies have, in fact, evidenced that background motion produces an asymmetric modulation of ongoing pursuit (Schwarz & Ilg, 1999), but the possibility that eye movements could explain away differences in psychophysical performance or provide a supplementary measure of recalibration was not investigated before. Figure 8 and Table 1 show the average smooth pursuit eye movement gain (eye velocity / target velocity) for Experiments 1 (Figure 8A) and 2 (Figure 8B). On the one hand, smooth pursuit gain over the 200 msec background motion period (marked in gray in Figure 8) was very similar across exposure and test trials and therefore cannot account for the differences in perception observed (see the average gains,  $M$ , and the associated confidence intervals,  $CI$  in Table 1). On the other hand, the pursuit gain is lower in Experiment 2 compared to Experiment 1, which might have to do with the general reduction in pursuit gain that takes place when flashing a stimulus during pursuit (Kerzel et al., 2010). Consistently with those findings, the pursuit gain after the background motion onset was higher in the experiment with the lowest motion energy (the contrast of the background motion pattern being much lower, as we had to filter light emanating from the screen), however we could also see that the gain is lower at the beginning of the background motion display. There could be a different trade-off of attentional resources to the perceptual and pursuit task, with more resources to the background in Experiment 2, as it was more salient.



**Figure 8.** Eye movement data expressed in terms of horizontal smooth pursuit eye movement gain as a function of time with respect to (w.r.t.) background motion onset. A. Results from Experiment 1 for the Exposure conditions with 5 deg/sec and -5 deg/sec speed for the background motion during exposure trials averaged for 7 participants. B. Results from Experiment 2, averaged for 8 participants, for the Exposure condition, where speed for the background motion during exposure trials was -5 deg/sec. In every panel, data is shown for exposure trials, test trials happening in the same VF as exposure and test trials in the opposite VF as exposure. The area in gray from 0 to 200 msec marks the background motion period.

<b>Experiment 1</b>					
<b>Control Same VF</b>	<b>Control Opposite VF</b>		<b>Exposure trials</b>	<b>Same VF</b>	<b>Opposite VF</b>
M=1.01, [CI: 0.94, 1.09], n=7	M=1.01, [CI:0.92, 1.10], n=7	<b>Exposure: 5 deg/sec</b>	M=1.00, [CI: 0.91, 1.08], n=7	M=0.99, [CI: 0.90, 1.10], n=7	M=1.01, [CI: 0.93,1.08], n=7
		<b>Exposure: -5 deg/sec</b>	M=1.01, [CI: 0.91, 1.12], n=7	M=1.00, [CI: 0.93, 1.07], n=7	M=1.00, [CI: 0.92,1.09], n=7

<b>Experiment 2</b>					
<b>Control Same VF</b>	<b>Control Opposite VF</b>		<b>Exposure trials</b>	<b>Same VF</b>	<b>Opposite VF</b>
M=0.85, [CI:0.77, 0.94], n=7	M=0.87, [CI:0.79, 0.94], n=7	<b>Exposure: -5 deg/sec</b>	M=0.84, [CI: 0.79, 0.89], n=8	M=0.83, [CI: 0.77, 0.88], n=8	M=0.82, [CI: 0.75,0.89], n=8

**Table 1.** Average smooth pursuit eye movement gain over the 200 msec background motion period, M, together with the associated confidence interval, CI, for the eye movement data from Experiments 1 and 2. Results are shown for the Control condition (where only test trials take place) and the Exposure condition (with both exposure and test trials). We refer to same VF or opposite VF depending on which visual field is exposed in the exposure condition, i.e. the same VF condition in the control condition refers to the VF that was exposed in the exposure condition.

## DISCUSSION

Eye movements introduce changes in the motion trajectories of the projected retinal images of real-life moving objects. There is a mismatch between the actual motion of a stimulus and its trajectory projected onto the retina during motion of the eyes. Thus, a mechanism informing about real objective motion by compensating for eye movements is necessary. Motion constancy can be achieved using an estimate of retinal motion and an estimate of eye movement velocity (Sperry 1950; von Holst and Mittelstaedt 1950; Haarmeier et al. 2001; Souman et al. 2006). However, eye velocity information (extraretinal information) has been demonstrated to be inaccurate (Bridgeman et al., 1994; Freeman et al., 2010). Therefore, it is unlikely that motion constancy solely depends on the previously reported computations compensating for eye movements. Indeed, Haarmeier et al. (2001) provided evidence for a constant updating of the estimation of the predicted reafference, which makes it possible to extract visual motion accurately. Namely, evidence for an image-based mechanism is reported, acting alongside the aforesaid compensation for eye movements. In particular, Haarmeier et al. (2001) showed how repeated exposure to background motion during pursuit shifts the PSS when judging the motion of a background drifting stimulus.

Here, following up on the study of Haarmeier et al. (2001), we have performed two experiments to shed light on how reafferent signals are used by the visual system to extract visual motion. Experiment 1, using much smaller stimuli (display area for background dots in Experiment 1: 4 x 30 deg, 6 deg eccentricity; Experiment 2: 9 x 30 deg at 6 deg eccentricity; Haarmeier Experiments

1-3: 42 x 38 deg), replicates the exposure effect observed by Haarmeier et al. (2001), with exposure to backward motion (-5 deg/sec). Such exposure effect can be appreciated as a shift in the PSS for the perception of background stimuli after repeated exposure has taken place. Besides, there is a strong initial bias in subjective stationarity, consistent with the classical Filehne effect, indicating underestimation of eye movement velocity (Filehne, 1922). On the other hand, no effect of exposure to forward motion was appreciated: the PSS given a repeatedly exposed background with a velocity of 5 deg/sec was close to the initial bias. Finally, for the first time, Experiment 1 has dealt with disentangling whether the mechanism responsible for the updating of the reference signal is global or not. In this regard, we found that the effect of exposure on PSS is at least specific to the visual field that is exposed. Specifically, there was a significant change compared to the control condition in the exposed visual field but not the unexposed visual field, suggesting that the updating of the reference signal concerns motion detectors covering a limited visual area, and therefore, is not a global mechanism.

Experiment 2 additionally confirms the exposure effect observed in Experiment 1 for -5 deg/sec background motion, as well as its specificity to the exposed visual field. Besides, it aimed to tell whether the updating mechanisms by which reafferent motion affects the PSS is due to recalibration account, contingent adaptation or both. A re-calibration model (Figure 1B) is favored when looking at the results of a detailed psychometric investigation, showing no change in sensitivity (i.e. slope) after exposure, but a shift in PSS. The rationale is that a change in sensitivity should have taken place provided a decrease in the sensitivity of the motion sensors due to their adaptation. Given no such change in sensitivity, evidence points to re-calibration rather than adaptation. Because of this, we may now use the term re-calibration rather than update or exposure effect. This interpretation is consistent with the finding that the retinal motion of the stationary background during pursuit results in no or only a weak motion aftereffect (Mack et al., 1987; Malkinson et al., 2012; Morgan et al., 1976). Consistently, Haarmeier et al. (2001) also found no motion aftereffect in their manipulation of background motion. Importantly, the eye movement results from Experiment 2, as well as Experiment 1, suggest that the differences between conditions seen in the psychophysical results are not caused by differences in pursuit eye movements. Finally, Experiment 2 we collected information about confidence judgements along with perceptual judgements. This way, we ruled out the possible effect of a gaze-contingent response bias (e.g. tending to respond in the exposed motion direction relative to the pursuit direction), because we found that globally the point of minimal confidence aligned with the PSS in all conditions. This method has been validated recently by Gallagher et al. (2019). Subjects are able to accurately report their own performance during perceptual decision tasks (Fleming et al., 2012; Fleming & Lau, 2014; Henmon, 1911; Maniscalco & Lau, 2012; Nelson, 1984; Yeung & Summerfield, 2012). As a consequence, confidence judgements are a valuable tool to tell apart perceptual changes from response biases. For instance, if an aftereffect were caused by a change in

sensory encoding, such aftereffect should have a similar impact both on categorical perceptual decisions and confidence judgements. Conversely, an aftereffect being caused by changes in decision making (M. Morgan et al., 2012; Yarrow et al., 2011) may influence perceptual decisions made under uncertainty; but no effects on the confidence of those decisions should be seen. This dissociation is the key to identify response biases. In our case, the reasoning goes that the uncertainty about a directional judgement should be maximal at the PSS since no leftward or rightward motion is seen, but not if the PSS shift results from a response bias. We should have seen a dissociation between those two estimates otherwise.

An interesting point of note is that the PSS in the control condition in Experiment 1 and Experiment 2 is similar despite large differences in the contrast of the stimulus. This is counterintuitive if we think of Bayesian model by Freeman et al. (2010), where the combination of eye movement estimates and retinal speed estimates depends on their respective uncertainty. In Experiment 1 the retinal motion uncertainty should be much higher than in Experiment 2. Perhaps this difference in uncertainty is small compared to the uncertainty of the eye movement estimate.

The mechanisms by which recalibration of re-afference during pursuit takes place could be understood within the type of Bayesian framework that has been used to model anticipatory pursuit (Orban de Xivry et al., 2013), in which pursuit of a target is driven by a sensory signal (the target motion) and an extra-retinal signal that represents the best prediction of the target motion based on past trials. A similar principle could be applied to re-afferent motion and it would be matter of future investigation to which extent a unitary process could account for both types of extra-retinal signals. We can note also that Harris, Morgan and Still (1981) have explained the effect of self-movement on the motion-aftereffect, under a similar framework, by considering that its primary cause is a sensory conflict, with a sizable portion of the visual field indicating self-motion while other extra-retinal cues indicate stationarity. Their argument is that because the world is mostly stationary, a major cause of retinal motion is observer movement or eye movements and then it is adaptive to update perceptual estimates. At least the motion aftereffect with a stationary test appears to confirm a similar prediction, showing a recalibration effect (a shift in “dipper” functions, or contrast discrimination thresholds versus pedestal contrast) but not a loss of sensitivity (Morgan et al., 2011). To sum up, the recalibration effect we measured may be the result of a very general mechanism (Morgan et al., 2011) by which sensory signals and extraretinal cues are used to produce a best guess based on stimulus history and the reliability of various sources of information (Freeman et al., 2010; e.g. Orban de Xivry et al., 2013).

Given the presence of neurons sensitive to motion in the world during pursuit (Duffy & Wurtz, 1991a; Graziano et al., 1994; Maunsell & Van Essen, 1983; Newsome et al., 1988; Saito et al., 1986; Sakata et al., 1983) and the presence of neurons encoding eye velocity (Komatsu & Wurtz, 1988;

Thier & Erickson, 1992), area MST would seem to provide the neural substrate for the effects we observe. Haarmeier et al. (2001) argued further that area MSTd (dorsal subdivision of the medial superior temporal area), where one finds neurons with large receptive fields responding to optic flow patterns (Bradley et al., 1996; Duffy & Wurtz, 1991b) could implement the recalibration of the reafferent signal. Some of the neurons recorded in MSTd are even able to compensate for changes induced by pursuit in retinal flow fields (Bradley et al., 1996; Shenoy et al., 1999). On the other hand, a different subset of neurons—visual tracking (VT) neurons—in MSTs (middle supratemporal sulcus), MSTl (lateral subdivision of the medial superior temporal area) and MSTd (dorso-medial part) encode extraretinal signals informing about eye velocity (Ilg & Thier, 2003; Komatsu & Wurtz, 1988; Newsome et al., 1988; Ono & Mustari, 2006; Thier & Erickson, 1992). Thus, the compensation for pursuit-induced changes carried out by optic flow neurons in MSTd may result from the action of VT neurons encoding extraretinal signals. In addition, a large subset of VT neurons show a response that is scaled with target velocity in world-centered coordinates, as they fire independently of the head or eye movements required to foveate the target (Ilg et al., 2004). In this regard, Haarmeier et al. (2001) suggested that VT neurons could aid recalibration by changing either their activity or the strength of their impact on MSTd optic flow neurons. Further investigations would be needed to specify whether recalibration affects eye velocity estimates as well as objective motion estimates, which would support the role of VT and optic flow neurons. It could also be that re-calibration is only visual. In any case, the neurons underlying recalibration need receptive fields that are small enough to fit the reported visual field specificity, meaning that they should either respond to one visual field or have a receptive field that stretches at most 10 deg, as to not to cover exposure and test stimuli presented in the upper and lower visual field. However, the typical receptive field size of dorsal and ventral MST is larger than 50 deg (dorsal) and 20-27 deg (ventral and intermediate regions of ventral MST) at a 6 deg eccentricity (their Figure 5; Tanaka et al., 1993). On the other hand, the typical receptive field size of MT neurons at the same eccentricity is of only 6 deg (Tanaka et al., 1993). Therefore, our study would suggest a locus of the recalibration effect that originates in MT or in the transmission of signals from MT to MST, which would allow for the spatially localized recalibration effect we observed. Although the speed tuning of neurons in MT does not compensate for reafferent input during pursuit as in area MST and therefore does not encode veridical object motion (Chukoskie & Movshon, 2009a; Inaba et al., 2007), MT neurons do show some suppression for motion opposite to pursuit direction (Chukoskie & Movshon, 2009). This gaze-contingent modulation of response gain might contribute to the veridical perception of motion during pursuit by suppressing reafferent motion signals and might also be the first processing stage where a recalibration process takes place.

## CONCLUSIONS

We show that the accuracy of the extraction of motion in the world depends on an image-based recalibration process, shifting the point of subjective stationarity without changing sensitivity to motion. This recalibration effect only takes place over the visual field being exposed to background motion.

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## REFERENCES

- Adelson, E. H., & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America A*, 2(2), 284. <https://doi.org/10.1364/JOSAA.2.000284>
- Adelson, E. H., & Movshon, J. A. (1982). Phenomenal coherence of moving visual patterns. *Nature*, 300(5892), 523–525. <https://doi.org/10.1038/300523a0>
- Anderson, S. J., Burr, D. C., & Morrone, M. C. (1991). Two-dimensional spatial and spatial-frequency selectivity of motion-sensitive mechanisms in human vision. *Journal of the Optical Society of America A. Optics and Image Science*, 8(8), 1340–1351.
- Anderson, Stephen J., & Burr, D. C. (1985). Spatial and temporal selectivity of the human motion detection system. *Vision Research*, 25(8), 1147–1154. [https://doi.org/10.1016/0042-6989\(85\)90104-X](https://doi.org/10.1016/0042-6989(85)90104-X)
- Anderson, Stephen J., & Burr, D. C. (1989). Receptive field properties of human motion detector units inferred from spatial frequency masking. *Vision Research*, 29(10), 1343–1358. [https://doi.org/10.1016/0042-6989\(89\)90191-0](https://doi.org/10.1016/0042-6989(89)90191-0)
- Anstis, S., & Casco, C. (2006). Induced movement: The flying bluebottle illusion. *Journal of Vision*, 6(10), 8. <https://doi.org/10.1167/6.10.8>
- Aubert, H. (1886). Die Bewegungsempfindung. *Pflügers Archiv European Journal of Physiology*, 39(1), 347–370.



- Bahill, A. T., & McDonald, J. D. (1983). Frequency Limitations and Optimal Step Size for the Two-Point Central Difference Derivative Algorithm with Applications to Human Eye Movement Data. *IEEE Transactions on Biomedical Engineering*, 30(3), 191–194. <https://doi.org/10.1109/TBME.1983.325108>
- Bell, C. C. (1981). An efference copy which is modified by reafferent input. *Science*. <https://doi.org/10.1126/science.7291985>
- Bradley, D. C., Maxwell, M., Andersen, R. A., Banks, M. S., & Shenoy, K. V. (1996). Mechanisms of heading perception in primate visual cortex. *Science*, 273(5281), 1544–1547.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10, 433–436.
- Bridgeman, B. (2007). Efference copy and its limitations. *Computers in Biology and Medicine*, 37(7), 924–929.
- Bridgeman, B., Van der Heijden, A. H. C., & Velichkovsky, B. M. (1994). A theory of visual stability across saccadic eye movements. *Behavioral and Brain Sciences*, 17(2), 247–258. <https://doi.org/10.1017/S0140525X00034361>
- Chukoskie, L., & Movshon, J. A. (2009a). Modulation of visual signals in macaque MT and MST neurons during pursuit eye movement. *Journal of Neurophysiology*, 102(6), 3225–3233. <https://doi.org/10.1152/jn.90692.2008>
- Chukoskie, L., & Movshon, J. A. (2009b). Modulation of Visual Signals in Macaque MT and MST Neurons During Pursuit Eye Movement. *Journal of Neurophysiology*, 102(6), 3225–3233. <https://doi.org/10.1152/jn.90692.2008>
- Cooper, E. A., Jiang, H., Vildavski, V., Farrell, J. E., & Norcia, A. M. (2013). Assessment of OLED displays for vision research. *Journal of Vision*, 13(12), 16. <https://doi.org/10.1167/13.12.16>
- Deubel, H., Koch, C., & Bridgeman, B. (2010). Landmarks facilitate visual space constancy across saccades and during fixation. *Vision Res*, 50(2), 249–259. <https://doi.org/10.1016/j.visres.2009.09.020>
- Duffy, C. J., & Wurtz, R. H. (1991a). Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. *Journal of Neurophysiology*. <https://doi.org/10.1152/jn.1991.65.6.1329>
- Duffy, C. J., & Wurtz, R. H. (1991b). Sensitivity of MST neurons to optic flow stimuli. II. Mechanisms of response selectivity revealed by small-field stimuli. *Journal of Neurophysiology*. <https://doi.org/10.1152/jn.1991.65.6.1346>

- Duncker, K. (1929). Über induzierte bewegung. *Psychologische Forschung*, 12(1), 180–259.
- Dürsteler, M. R. (2014). A common framework for the analysis of complex motion? Standstill and capture illusions. *Frontiers in Human Neuroscience*, 8. <https://doi.org/10.3389/fnhum.2014.00999>
- Filehne, W. (1922). Über das optische Wahrnehmen von Bewegungen. *Zeitschrift Für Sinnesphysiologie*, 53, 134–144.
- Fleming, S. M., Dolan, R. J., & Frith, C. D. (2012). Metacognition: Computation, biology and function. In *Philosophical Transactions of the Royal Society B: Biological Sciences*. <https://doi.org/10.1098/rstb.2012.0021>
- Fleming, S. M., & Lau, H. C. (2014). How to measure metacognition. In *Frontiers in Human Neuroscience*. <https://doi.org/10.3389/fnhum.2014.00443>
- 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>
- Fukutomi, M., & Carlson, B. A. (2020). A History of Corollary Discharge: Contributions of Mormyrid Weakly Electric Fish. In *Frontiers in Integrative Neuroscience*. <https://doi.org/10.3389/fnint.2020.00042>
- Gallagher, R. M., Suddendorf, T., & Arnold, D. H. (2019). Confidence as a diagnostic tool for perceptual aftereffects. *Scientific Reports*. <https://doi.org/10.1038/s41598-019-43170-1>
- Graziano, M. S. A., Andersen, R. A., & Snowden, R. J. (1994). Tuning of MST neurons to spiral motions. *Journal of Neuroscience*. <https://doi.org/10.1523/jneurosci.14-01-00054.1994>
- Haarmeier, T., Bunjes, F., Lindner, A., Berret, E., & Thier, P. (2001). Optimizing visual motion perception during eye movements. *Neuron*, 32(3), 527–535. [https://doi.org/10.1016/S0896-6273\(01\)00486-X](https://doi.org/10.1016/S0896-6273(01)00486-X)
- Harris, L. R., Morgan, M. J., & Still, A. W. (1981). Moving and the motion after-effect. *Nature*. <https://doi.org/10.1038/293139a0>
- Henmon, V. A. C. (1911). The relation of the time of a judgement to its accuracy. *Psychological Review*. <https://doi.org/10.1037/h0074579>
- Honda, H. (1990). The extraretinal signal from the pursuit-eye-movement system: Its role in the perceptual and the egocentric localization systems. *Perception & Psychophysics*.

<https://doi.org/10.3758/BF03211595>

- Ilg, U. J., Schumann, S., & Thier, P. (2004). Posterior parietal cortex neurons encode target motion in world-centered coordinates. *Neuron*, 43(1), 145–151. <https://doi.org/10.1016/j.neuron.2004.06.006>
- Ilg, U. J., & Thier, P. (2003). Visual tracking neurons in primate area MST are activated by smooth-pursuit eye movements of an “imaginary” target. *Journal of Neurophysiology*, 90(3), 1489–1502. <https://doi.org/10.1152/jn.00272.2003>
- Inaba, N., Shinomoto, S., Yamane, S., Takemura, A., & Kawano, K. (2007). MST neurons code for visual motion in space independent of pursuit eye movements. *Journal of Neurophysiology*, 97(February 2007), 3473–3483. <https://doi.org/10.1152/jn.01054.2006>
- Kerzel, D., Born, S., & Souto, D. (2010). Inhibition of steady-state smooth pursuit and catch-up saccades by abrupt visual and auditory onsets. *Journal of Neurophysiology*, 104(5), 2573–2585. <https://doi.org/10.1152/jn.00193.2010>
- Kleiner, M., Brainard, D. H., & Pelli, D. G. (2007, August). *What’s new in Psychtoolbox-3?*
- Kohn, A. (2007). Visual adaptation: physiology, mechanisms, and functional benefits. *J Neurophysiol*, 97(5), 3155–3164. [http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list\\_uids=17344377](http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=17344377)
- Kohn, A., & Movshon, J. A. (2003). Neuronal adaptation to visual motion in area MT of the macaque. *Neuron*, 39(4), 681–691. [http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list\\_uids=12925281](http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=12925281)
- Komatsu, H., & Wurtz, R. H. (1988). Relation of cortical areas MT and MST to pursuit eye movements. I. Localization and visual properties of neurons. *J Neurophysiol*, 60(2), 580–603.
- Lee, B., Pesaran, B., & Andersen, R. A. (2011). Area MSTd Neurons Encode Visual Stimuli in Eye Coordinates During Fixation and Pursuit. *Journal of Neurophysiology*, 105(1), 60–68. <https://doi.org/10.1152/jn.00495.2009>
- Mack, A., Goodwin, J., Thordarsen, H., Benjamin, D., Palumbo, D., & Hill, J. (1987). Motion aftereffects associated with pursuit eye movements. *Vision Research*, 27(4), 529–536. [https://doi.org/10.1016/0042-6989\(87\)90039-3](https://doi.org/10.1016/0042-6989(87)90039-3)
- Mack, A., & Herman, E. (1978). The loss of position constancy during pursuit eye movements. *Vision*

*Research*, 18(1), 55–62. [https://doi.org/10.1016/0042-6989\(78\)90077-9](https://doi.org/10.1016/0042-6989(78)90077-9)

- Malkinson, T. S., McKyton, A., & Zohary, E. (2012). Motion adaptation reveals that the motion vector is represented in multiple coordinate frames. *Journal of Vision*. <https://doi.org/10.1167/12.6.30>
- Maniscalco, B., & Lau, H. (2012). A signal detection theoretic approach for estimating metacognitive sensitivity from confidence ratings. *Consciousness and Cognition*. <https://doi.org/10.1016/j.concog.2011.09.021>
- Mateeff, S., Dimitrov, G., Genova, B., Likova, L., Stefanova, M., & Hohnsbein, J. (2000). The discrimination of abrupt changes in speed and direction of visual motion. *Vision Research*. [https://doi.org/10.1016/S0042-6989\(99\)00185-6](https://doi.org/10.1016/S0042-6989(99)00185-6)
- Maunsell, J. H. R., & Van Essen, D. C. (1983). Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. *Journal of Neurophysiology*. <https://doi.org/10.1152/jn.1983.49.5.1127>
- Mayhew, J. E. W. (1973). After-effects of movement contingent on direction of gaze. *Vision Research*. [https://doi.org/10.1016/0042-6989\(73\)90051-5](https://doi.org/10.1016/0042-6989(73)90051-5)
- Morgan, M., Dillenburger, B., Raphael, S., & Solomon, J. A. (2012). Observers can voluntarily shift their psychometric functions without losing sensitivity. *Attention, Perception, & Psychophysics*, 74(1), 185–193. <https://doi.org/10.3758/s13414-011-0222-7>
- Morgan, M. J., Chubb, C., & Solomon, J. A. (2011). Evidence for a subtractive component in motion adaptation. *Vision Research*, 51(21–22), 2312–2316. <https://doi.org/10.1016/j.visres.2011.09.002>
- Morgan, M., Ward, R. M., & Brussell, E. M. (1976). The Aftereffect of Tracking Eye Movements. *Perception*, 5(3), 309–317. <https://doi.org/10.1068/p050309>
- Murakami, I., & Cavanagh, P. (1998). A jitter after-effect reveals motion-based stabilization of vision. *Nature*, 395(6704), 798–801. <https://doi.org/10.1038/27435>
- Murakami, I., & Cavanagh, P. (2001). Visual jitter: evidence for visual-motion-based compensation of retinal slip due to small eye movements. *Vision Research*, 41(2), 173–186. <http://www.ncbi.nlm.nih.gov/pubmed/11163852>
- Nelson, T. O. (1984). A comparison of current measures of the accuracy of feeling-of-knowing predictions. *Psychological Bulletin*. <https://doi.org/10.1037/0033-2909.95.1.109>
- Newsome, W. T., Wurtz, R. H., & Komatsu, H. (1988). Relation of cortical areas MT and MST to pursuit eye movements. II. Differentiation of retinal from extraretinal inputs. *Journal of*

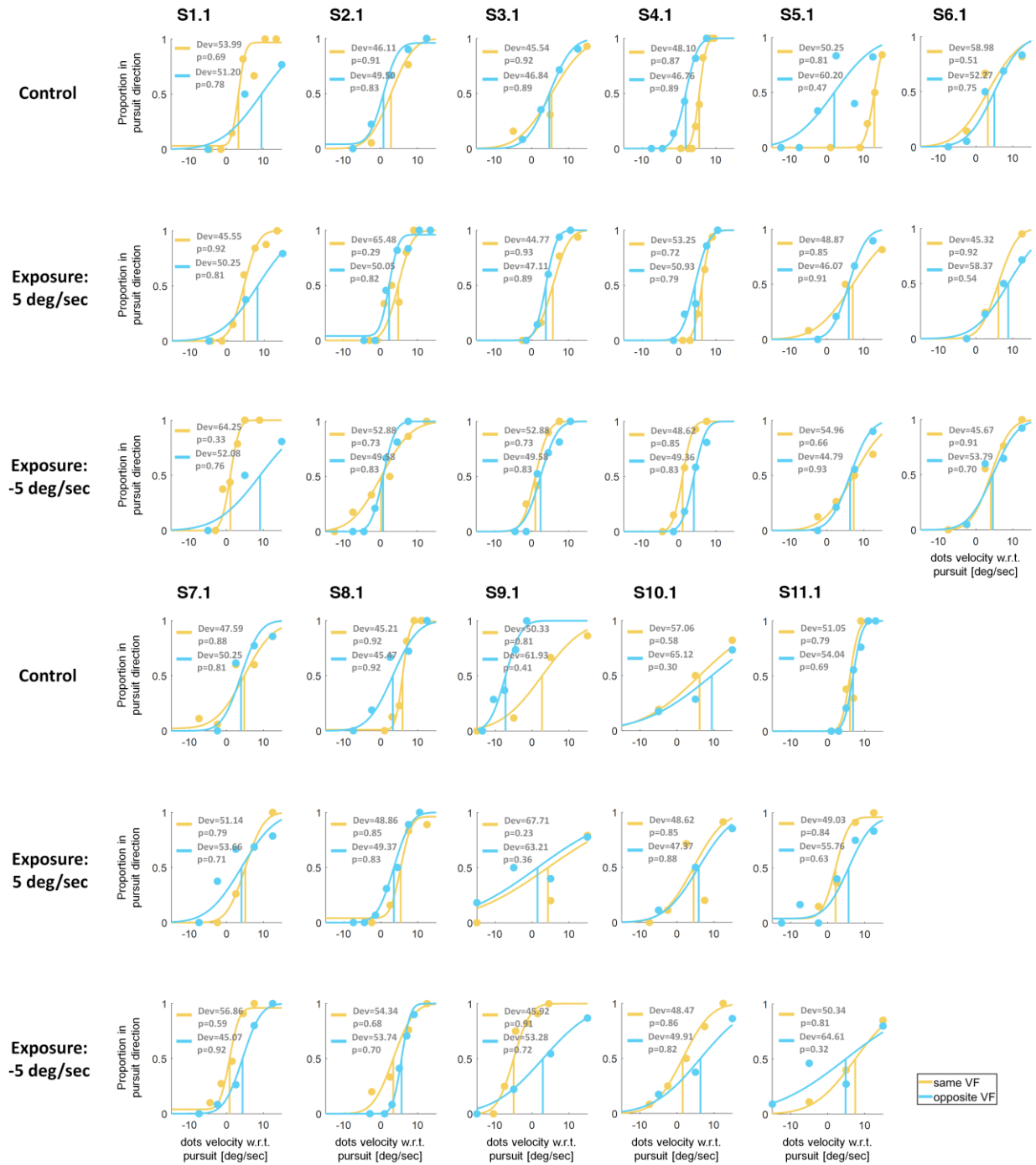
*Neurophysiology*, 60(2), 604–620. <https://doi.org/10.220.33.5>

- Nishida, S., Motoyoshi, I., Andersen, R. A., & Shimojo, S. (2003). Gaze modulation of visual aftereffects. *Vision Res*, 43(6), 639–649. <http://www.ncbi.nlm.nih.gov/pubmed/12604100>
- Ono, S., & Mustari, M. J. (2006). Extraretinal signals in MSTd neurons related to volitional smooth pursuit. *Journal of Neurophysiology*, 96(5), 2819–2825. <https://doi.org/10.1152/jn.00538.2006>
- Orban de Xivry, J. J., Coppe, S., Blohm, G., & Lefevre, P. (2013). Kalman filtering naturally accounts for visually guided and predictive smooth pursuit dynamics. *J Neurosci*, 33(44), 17301–17313. <https://doi.org/10.1523/JNEUROSCI.2321-13.2013>
- Parwaga, S., Buckley, D., & Duke, P. A. (2016). Tilt representation beyond the retinotopic level. *Journal of Vision*. <https://doi.org/10.1167/16.3.11>
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10, 437–442.
- Pelz, J. B., & Hayhoe, M. M. (1995). The role of exocentric reference frames in the perception of visual direction. *Vision Res*, 35(16), 2267–2275. <http://www.ncbi.nlm.nih.gov/pubmed/7571463>
- Poletti, M., Listorti, C., & Rucci, M. (2010). Stability of the Visual World during Eye Drift. *Journal of Neuroscience*, 30(33), 11143–11150. <https://doi.org/10.1523/JNEUROSCI.1925-10.2010>
- Raghuandan, A., Frasier, J., Poonja, S., Roorda, A., & Stevenson, S. B. (2008). Psychophysical measurements of referenced and unreferenced motion processing using high-resolution retinal imaging. *Journal of Vision*, 8(14), 14 1-11. <https://doi.org/10.1167/8.14.14>
- Saito, H. A., Yukie, M., Tanaka, K., Hikosaka, K., Fukada, Y., & Iwai, E. (1986). Integraton of direction signals of image motion in the superior temporal sulcus of the Macaque monkey. *Journal of Neuroscience*. <https://doi.org/10.1523/jneurosci.06-01-00145.1986>
- Sakata, H., Shibutani, H., & Kawano, K. (1983). Functional properties of visual tracking neurons in posterior parietal association cortex of the monkey. *Journal of Neurophysiology*. <https://doi.org/10.1152/jn.1983.49.6.1364>
- Schlack, A., Krekelberg, B., & Albright, T. D. (2007). Recent history of stimulus speeds affects the speed tuning of neurons in area MT. *Journal of Neuroscience*. <https://doi.org/10.1523/JNEUROSCI.3165-07.2007>
- Schwarz, U., & Ilg, U. (1999). Asymmetry in visual motion processing. *Neuroreport*, 10(12), 2477–2480. <http://www.ncbi.nlm.nih.gov/pubmed/10574355>

- Shen, Y., Dai, W., & Richards, V. M. (2015). A MATLAB toolbox for the efficient estimation of the psychometric function using the updated maximum-likelihood adaptive procedure. *Behavior Research Methods*. <https://doi.org/10.3758/s13428-014-0450-6>
- Shenoy, K. V., Bradley, D. C., & Andersen, R. A. (1999). Influence of gaze rotation on the visual response of primate MSTd neurons. *Journal of Neurophysiology*, *81*(6), 2764–2786. <http://www.ncbi.nlm.nih.gov/pubmed/10368396>
- Souman, J., Hooge, I., & Wertheim, A. (2006). Frame of reference transformations in motion perception during smooth pursuit eye movements. *Journal of Computational Neuroscience*, *20*(1), 61–76. <https://doi.org/10.1007/s10827-006-5216-4>
- Souto, D., Chudasama, J., Kerzel, D., & Johnston, A. (2019). Motion integration is anisotropic during smooth pursuit eye movements. *Journal of Neurophysiology*. <https://doi.org/10.1152/jn.00591.2018>
- Souto, D., Gegenfurtner, K. R., & Schütz, A. C. (2016). Saccade Adaptation and Visual Uncertainty. *Frontiers in Human Neuroscience*, *10*, 1–12. <https://doi.org/10.3389/fnhum.2016.00227>
- 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>
- Sperry, R. W. (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. *J Comp Physiol Psychol*, *43*(6), 482–489.
- Tanaka, K., Sugita, Y., Moriya, M., & Saito, H. A. (1993). Analysis of object motion in the ventral part of the medial superior temporal area of the macaque visual cortex. *Journal of Neurophysiology*. <https://doi.org/10.1152/jn.1993.69.1.128>
- Terao, M., & Nishida, S. (2020). Direction of Apparent Motion During Smooth Pursuit Is Determined Using a Mixture of Retinal and Objective Proximities. *I-Perception*, *11*(3), 204166952093732. <https://doi.org/10.1177/2041669520937320>
- Thier, P., & Erickson, R. G. (1992). Responses of Visual-Tracking Neurons from Cortical Area MST-I to Visual, Eye and Head Motion. *European Journal of Neuroscience*, *4*(6), 539–553. [http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list\\_uids=12106340](http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=12106340)
- von Fleischl, E. (1882). Physiologisch-optische notizen. *Sitzung Wiener Bereich Der Akademie Der Wissenschaften*, *3*, 7–25.

- von Holst, E., & Mittelstaedt, H. (1950). Das reafferenzprinzip. *Naturwissenschaften*, 37(20), 464–476.
- Weiss, Y., Simoncelli, E. P., & Adelson, E. H. (2002). Motion illusions as optimal percepts. *Nat Neurosci*, 5(6), 598–604. <https://doi.org/10.1038/nn858>
- Wichmann, A. F., & Hill, N. J. (2001). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics*, 63(8), 1293–1313. <https://doi.org/10.3758/BF03194544>
- Wolpert, D. M., Diedrichsen, J., & Flanagan, J. R. (2011). Principles of sensorimotor learning. *Nat Rev Neurosci*, 12(12), 739–751. <https://doi.org/10.1038/nrn3112>
- Yarrow, K., Jahn, N., Durant, S., & Arnold, D. H. (2011). Shifts of criteria or neural timing? The assumptions underlying timing perception studies. *Consciousness and Cognition*. <https://doi.org/10.1016/j.concog.2011.07.003>
- Yeung, N., & Summerfield, C. (2012). Metacognition in human decision-making: Confidence and error monitoring. In *Philosophical Transactions of the Royal Society B: Biological Sciences*. <https://doi.org/10.1098/rstb.2011.0416>

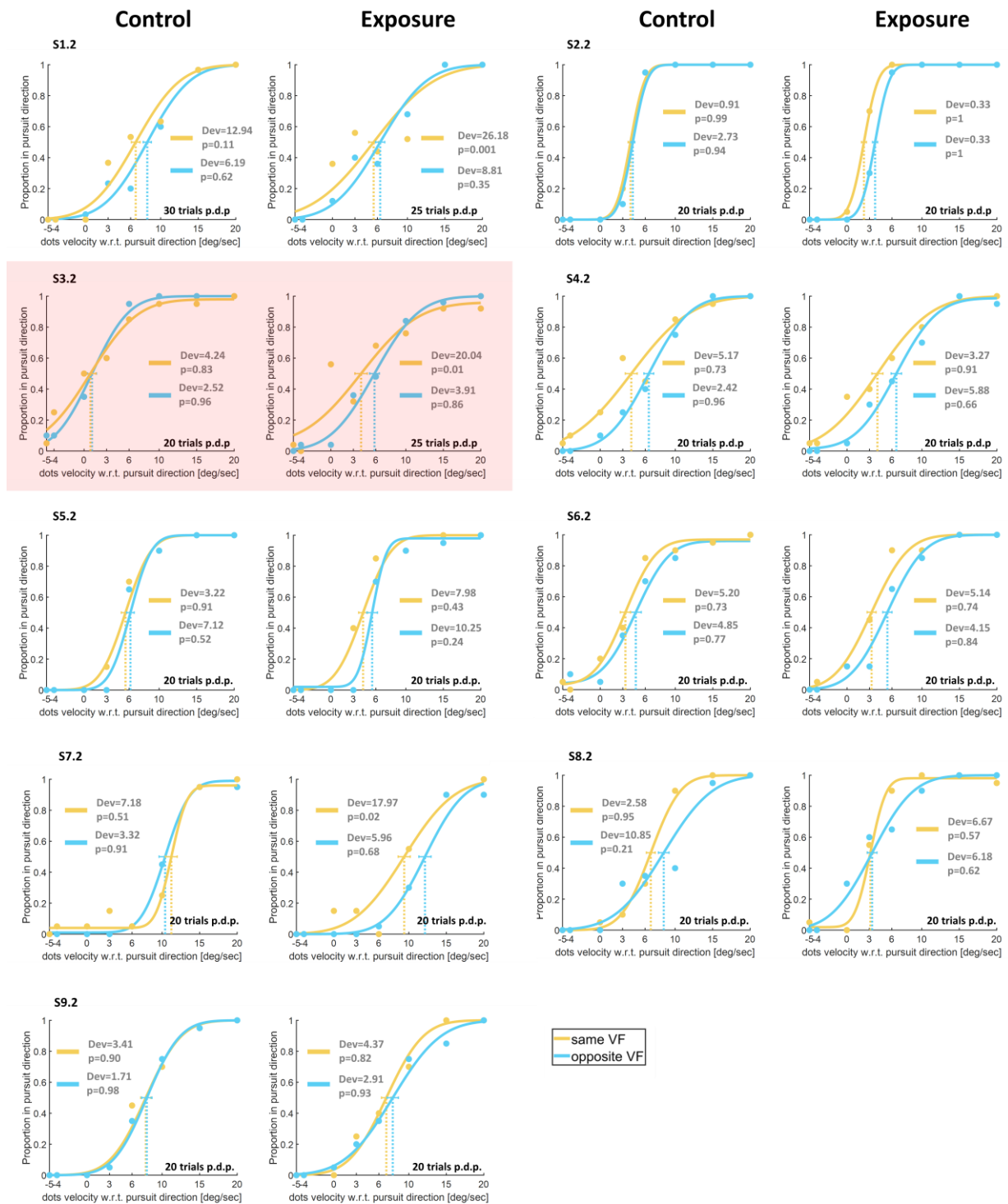
## APPENDIX A



**Figure A.1.** Results and psychometric function fits for the participants in Experiment 1 (from S1.1 to S11.1). Data is shown for the control (upper panels) and exposure conditions where observers were exposed to 5 deg/sec (middle-panels) and -5 deg/sec background motion (lower panels) relative to the pursuit direction. The x-axis represents dots velocity with respect to (w.r.t.) the pursuit direction, with positive values indicating that dots move in the direction of pursuit, negative values that they move opposite to pursuit. Each dot represents a binned proportion of responses for visualization. The vertical lines indicate the PSS, i.e. the point at which there is an equal proportion of responses in either direction. We refer to the same VF or opposite VF condition,



depending on which visual field is exposed in the exposure conditions, i.e. the same VF condition in the control condition refers to the VF that was exposed in the exposure condition. For each individual's psychometric functions, the Deviance and associated p-value is shown as an indicator of goodness of fit. Note that we used the same fitting procedure as in Experiment 2, but here every level was different. Therefore we binned the data for display (to eyeball the quality of the fits) by using the *histogram* function in Matlab (R2018a), with the default binning method ("auto"). Therefore, Deviance values are based on the number of observations determining the psychometric functions and not the number of dots that are displayed (unlike Experiment 2 where we used fixed levels).



**Figure A.2.** Results and psychometric function fits for the participants in Experiment 2 (from S1.2 to S9.2). The proportion of directional judgements in the direction of pursuit as a function of background velocity (dots velocity with respect to [w.r.t.] pursuit direction) is shown both for the control and exposure conditions. The vertical lines indicate the PSS, i.e. the point at which there is an equal proportion of responses in either direction. We refer to the same VF or opposite VF condition, depending on which visual field is exposed in the exposure conditions, i.e. the same VF condition in the control condition refers to the VF that was exposed in the exposure condition. In all plots, horizontal lines designate the  $\pm$ SD of the PSS. Non-parametric bootstrap was used to

calculate the SD of the PSS estimate. For each individual's psychometric functions, the number of trials per data point [p.d.p.] is specified, as well as each psychometric function's Deviance and associated p-value as an indicator of goodness of fit. Highlighted in red is subject S3.1, who was excluded from the analyses because of showing a strong shift in PSS (compared to control) opposite to everyone else.