

**Motion processing across spatial and temporal scales  
for human perception and eye movements**

by

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B.S., Peking University, 2015

M.A., New York University, 2017

A THESIS SUBMITTED IN PARTIAL FULFILLMENT  
OF THE REQUIREMENTS FOR THE DEGREE OF

**Doctor of Philosophy**

in

THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

(Neuroscience)

The University of British Columbia

(Vancouver)

June 2022

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# Abstract

We live in a dynamic visual environment, which requires perceiving moving objects around us and acting accordingly. However, we do not yet fully understand how visual information informs perception and motor actions. This dissertation examines the perception-action link by testing how motion and expectation signals are processed for perception and for eye movements as an example of human motor action.

I focus on two types of human eye movements triggered by distinct brain mechanisms: ocular torsion, the eyes' rotation about the line of sight triggered by rotational motion, and smooth pursuit, the eyes' continuous tracking of translational motion. Torsion is mostly controlled by subcortical brain areas, but might share early-stage cortical processing of sensory signals with perception. In contrast, smooth pursuit is controlled by subcortical and cortical areas and might therefore be more closely linked to perception, sharing both motion and expectation signal processing with perception.

To test the torsion-perception link, I utilized a perceptual illusion induced by visual rotational motion. Results show that torsional velocity correlates with the perceptual illusion, potentially suggesting shared motion processing (Chapter 2.1). However, anticipatory torsion can only be elicited by trial repetition, but not by cognitive cues that induce expectation (Chapter 2.2). These results show that similar visual motion signals might drive reflexive torsion and perception. Expectation signals appear to be less effective in driving torsion.

Probing the pursuit-perception link, I found dissociations between how each system processes motion and expectation signals. When integrating diverse motion signals across space, pursuit was biased to the average motion direction, whereas perception showed no consistent bias (Chapter 3). When investigating the role of expectation, I found that anticipatory pursuit followed the expected direction, whereas perception was biased in the opposite direction (Chapter 4).

Overall, this dissertation reveals that perception and eye movements likely share early-stage motion processing, even for reflexive eye movements such as torsion. But perception and eye movements differ in how they utilize higher-level motion or expectation signals. The dissociations might indicate how each system optimally meets different functional demands: Perception relies on object segregation, whereas eye movements rely on signal integration.

# Lay Summary

We constantly encounter moving objects in our daily lives, and need to judge and react to their direction and speed. However, our action is not necessarily based on the motion we consciously perceive. I investigate how perception and action are related, by examining the relationship between motion perception and two types of eye movements in response to visual motion. Under simple motion conditions, even a type of seemingly reflexive eye movement is correlated with perception. In contrast, perception and eye movements respond differently when assessing more complex motion signals presented across space and time. Overall, this work shows that perception and eye movements likely share the initial motion processing, but differ in further processing of signals based on their specific needs. Perception strives to segregate the object from the scene, whereas eye movements integrate all signals to maximize information collection.

# Preface

I was the lead on three out of four studies (Chapter 2.1, 3, and 4) presented in this thesis. In these studies, my responsibilities included all aspects of experimental design, procedure programming, data collection, analysis, interpretation, and manuscript composition. For the study presented in Chapter 2.2, I was responsible for Experiment 3, including experimental design, procedure programming, data collection, analysis, interpretation, and manuscript revision after initial peer review. Miriam Spering supervised all aspects of this thesis and provided feedback and edits to the manuscripts that resulted from this work. All studies were approved by the UBC Behavioural Research Ethics Board, certificates H11-00967 (Chapter 2), H20-02656 (Chapter 3), and H19-00994 (Chapter 4).

**Chapter 2.** A version of the study presented in Chapter 2.1 has been published as Wu, X. and Spering, M. (2019). Ocular torsion is related to perceived motion-induced position shifts. *Journal of Vision*, 19(12):1–13. XW collected and analyzed the data. XW and MS interpreted the data, wrote and revised the manuscript. A version of the study presented in Chapter 2.2 has been published as Rothwell, A. C., Wu, X., Edinger, J., and Spering, M. (2020). On the relation between anticipatory ocular torsion and anticipatory smooth pursuit. *Journal of vision*, 20(2):1–12. ACR was an undergraduate student under the supervision of MS, and collected and analyzed data for Experiment 1 and 2. XW collected and analyzed data for Experiment 3, which addressed the reviewer’s concerns of the initial manuscript. All authors interpreted the data. ACR, XW, and MS wrote the manuscript. XW and MS revised the manuscript.

**Chapter 3.** This study is currently under peer-review for publication in a journal. A version of this study has been presented as a poster in May 2022 at the 32nd CVS Symposium, Active Vision, organized by the Center for Visual Science (CVS) at the University of Rochester, NY, USA. XW collected and analyzed data. XW and MS interpreted the data and wrote the manuscript.

**Chapter 4.** A version of the study presented has been published as Wu, X., Rothwell, A. C., Spering, M., and Montagnini, A. (2021). Expectations about motion direction affect perception and anticipatory smooth pursuit differently. *Journal of Neurophysiology*, 125, 977–991. XW collected and analyzed data. XW, MS, and AM interpreted the data, wrote and revised the manuscript. ACR was an undergraduate student under the supervision of MS and AM, and was involved in the preliminary piloting of the experimental paradigm.

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# Acknowledgments

I would like to begin by acknowledging that the land on which we gather is the traditional, ancestral, and unceded territory of the  $x^w m\theta k^w \acute{a}y\acute{e}m$  (Musqueam) People (see [Musqueam & UBC](#)).

Foremost, I would like to give my sincere gratitude to my supervisor, Miriam. This work is not possible without your help. Thank you for all the guidance and support in conducting research, networking, presenting, and writing. Thank you for opening the academic world to me. What a journey of five years! I will carry on with what I have learned both in science and in life.

I would also like to express my gratitude to my supervisory committee, Debbie Giaschi, Jim Enns, and Jason Barton. Thank you for providing insightful guidance through my PhD study, and thought-provoking comments for my thesis. You have helped broaden my view both philosophically and scientifically.

Then, a huge thank you to Professor Anna Montagnini, who co-supervised me on the study presented in Chapter 4. I appreciate all the thoughtful discussions directly addressing my concerns and confusions. I still miss my visit to Marseille, where I received warm welcome and had a productive and exciting month.

I cannot be more grateful for the scientific/life inspiration and friendly support received from lab members. Jolande, I think my life direction has changed, in a good way, because of you. And no more poster tube accidents (so far)! Philipp, the best neighbour to have! You do know how to do good science, and how to make masterpiece bakery/hat! Doris, thanks for all the chats and support with genuine care. You will be a great mentor. Anouk, happy to see you starting an exciting job! Austin, Pearson, and Rose, thank you for making my first year at UBC delightful. Leah and Juana, thank you for bringing fresh spirits in the lab.

Finally, friends and family. A dear thank you to Moshi Li, who offered generous help in proofreading my thesis. Hope we both start an exciting journey after graduation. A heartfelt thank you to my parents, who have always been supporting and encouraging me to live a happy life. It is not an easy goal, but I am happy to see my dad still teaching students and leading research with enthusiasm, and my mom enjoying her retirement life. Then, Yuchi, thanks for accompanying me all the way. Thanks for taking care of me when I cannot, and being the shiny star in my sky. Let us keep checking off items from that lifelong to-do list.

The work in this dissertation is supported by a UBC Four-Year fellowship to X.W., a Natural Sciences and Engineering Research Council of Canada Discovery Grant and Accelerator Supplement and a UBC Centre for Brain Health grant to M.S., and a Centre National pour la Recherche Scientifique–Projet International de Cooperation Scientifique Grant to A.M.

# Chapter 1

## Introduction

*Considering Perception and Action as two global and independent entities has been a fertile scientific approach. Maybe the time has come to consider them as intimately related and to try to understand why and how different [factors](...) affect the observed performance.*  
— Cardoso-Leite and Gorea (2010), p.134

We constantly encounter moving objects in the environment, such as birds flying across the sky and cars passing on the street. To navigate through and interact with these highly dynamic visual surroundings, we rely on accurate perception of object motion. For example, we judge the speed of an oncoming car to decide when to cross the street, and we predict the trajectory of a ball in order to catch it. Intuitively, our actions should be based on and guided by our perception of the visual world (Clark, 2001). However, perception and action are two processes that do not necessarily rely on the same internal representation of the visual world around us. Visual perception and motor action can respond differently to the same visual stimuli (Cardoso-Leite and Gorea, 2010; Goodale and Milner, 1992; Spering and Carrasco, 2015). Even though perception and action are basic ways for us to process and respond to the environment, our understanding of their relationship is far from complete.

The overarching goal of this dissertation is to probe the perception-action relationship by testing how signals across spatial and temporal scales are processed for perception and action outcomes. Specifically, I will investigate and compare how motion perception and eye movements process visual motion and expectation signals. I manipulated visual motion signals from small-scale, internal motion to large-scale, object motion (across space), and expectation signals based on cognitive cues or past visual events (across time). The results will further our understanding of the extent to which perception and action share processing of signals to represent the world.

In the following Introduction sections, I will first talk about the evolving view of the dual visual systems framework (Goodale and Milner, 1992; Goodale and Westwood, 2004; Milner and Goodale, 2008), and how the investigation of motion perception and eye movements as examples of perception and action can add to our understanding of the nature of the perception-action relationship (Section 1.1). Next, I will introduce two types of continuous eye movements my dissertation work has focused on, torsional eye movements and

smooth pursuit eye movements (Section 1.2). In Section 1.3, I will summarize the state of the literature on the relationship between motion perception and eye movements, and identify open questions to be addressed in this dissertation. I will then review in Section 1.4 the neural pathways of smooth pursuit and torsion, and where connections to motion perception may occur. In the concluding section, I will provide an overview of the four experimental studies presented in this dissertation (Section 1.5).

## **1.1 The visual perception-action link**

Understanding how we perceive and move is fundamental in understanding how we interact with the world. For example, under what conditions do perception and action systems respond similarly? When will they be dissociated, if at all, and why? Before answering these questions, because the terms perception and action are two abstract concepts that require accurate definitions, I would like to first clarify their definitions in this dissertation. I follow the consensus of how these terms are viewed in experimental psychology. Perception refers to the conscious experience of visual stimuli, and action refers to the implementation of a movement (Milner and Goodale, 2008). Below, I will start with a general overview of the dual visual systems hypothesis, then explain the role of motion perception and eye movements in the perception-action link.

### **1.1.1 The dual visual systems hypothesis**

Whereas an intuitive and traditional view of the relationship between perception and action is that we act based on what we perceive (Clark, 2001), the dual visual systems hypothesis has been proposed and developed over decades to argue that visual information is processed differently for perception and action (Goodale, 2011; Goodale et al., 2005; Goodale and Milner, 1992; Goodale and Westwood, 2004; Milner and Goodale, 2008; Ungerleider and Mishkin, 1982). The initial framework consisted of two distinctive visual cortical pathways—a ventral pathway for object identification (“what”), and a dorsal pathway for spatial localization (“where”; Ungerleider and Mishkin 1982). The most representative supporting evidence is a double dissociation observed in the behaviour of patients with brain damage. For example, a patient with damage in the occipitotemporal region can hardly recognize the orientation of objects, but have accurate hand movements when reaching for the same objects (Goodale et al., 1991). On the other hand, patients with damage in the posterior parietal region have difficulty reaching for objects oriented at different angles, but can correctly indicate their orientations verbally (Perenin and Vighetto, 1988). Goodale and Milner (1992) emphasized the importance of the outcome requirements, recognizing orientation vs. reaching, instead of focusing on the input properties (object shape vs. location), expanding the dual visual pathways view to “what” vs. “how”, or “vision-for-perception” vs. “vision-for-action”. Visual inputs are received on the retina and projected through the lateral geniculate nucleus (LGN) to the primary visual cortex (V1) for both visual pathways. The dual visual pathways then separate after V1, reaching to either the inferotemporal cortex (ventral) or the posterior parietal region (dorsal), serving different functional purposes.

However, perception and action are not completely independent, but interact and cooperate (Goodale,

2011; Goodale et al., 2005; Goodale and Westwood, 2004; Milner and Goodale, 2008). For example, grasping posture is affected by object functionality (e.g., always grasping the handle of a toothbrush) regardless of how awkward the wrist rotation might be (Creem and Proffitt, 2001), suggesting that the perceptual system is involved in selecting the specific action type (Kilner, 2011). The dorsal pathway has also been suggested to contribute to non-action-based perceptual representations (Freud et al., 2016). To understand the extent of processing being shared by perception and action, a direct comparison of responses from both systems is necessary under different stimulus and task conditions, in which signals from multiple sources across space and/or across time are involved.

### **1.1.2 Studying the perception-action link with motion perception and eye movements**

Motion perception and eye movements are ubiquitous in our daily lives. However, many studies have focused on perception of static objects (but see the double-step paradigm, e.g., Goodale et al. 1986), and it is not easy to fit motion perception and eye movements in the classical dual visual systems framework of separating pathways after V1 (Goodale, 2011; Goodale et al., 2005; Goodale and Westwood, 2004; Milner and Goodale, 2008). The major cortical areas processing visual motion input in primates are the middle temporal (MT) and the adjacent medial superior temporal (MST) areas (Britten et al., 1996; Celebrini and Newsome, 1994; Maunsell and Van Essen, 1983b; Mikami et al., 1986; Rudolph and Pasternak, 1999), also referred to as MT+/V5 in human (Huk et al., 2002; Tootell et al., 1995; Watson et al., 1993). MT has often been attributed to the dorsal pathway in the dual visual systems framework (Goodale and Milner, 1992; Goodale and Westwood, 2004). But MT serves important roles in motion perception irrespective of a following action, and is also likely to perform high-level processing, such as the integration and segmentation of complex motion stimuli (Born and Bradley, 2005; Gilaie-Dotan, 2016; Zeki, 2015). Eye movements are special in that they do not directly interact with the environment like other motor actions do (e.g., using the hand to pick up an apple). They constantly modify the visual image on the retina, with a direct impact on perception (Rolfs and Schweitzer, 2022). Even the tiny-scale eye movements that occur during fixation help reformat retinal inputs so that our neural system can better process them (Rucci et al., 2018). Motion perception and eye movements are two key responses to our dynamic visual environment. Studying the relationship between motion perception and eye movements can provide insights into the perception-action link complementary to the link between perception and motor actions that directly interact with the world.

In the following sections, I will discuss the relationship between perception and different types of eye movements based on their functional purposes, and identify open questions in this area of research. By studying the relationship between motion perception and eye movements, I hope to further the understanding of how different signals across space and time are processed to shape perception and guide action.

## 1.2 Functional role of eye movements

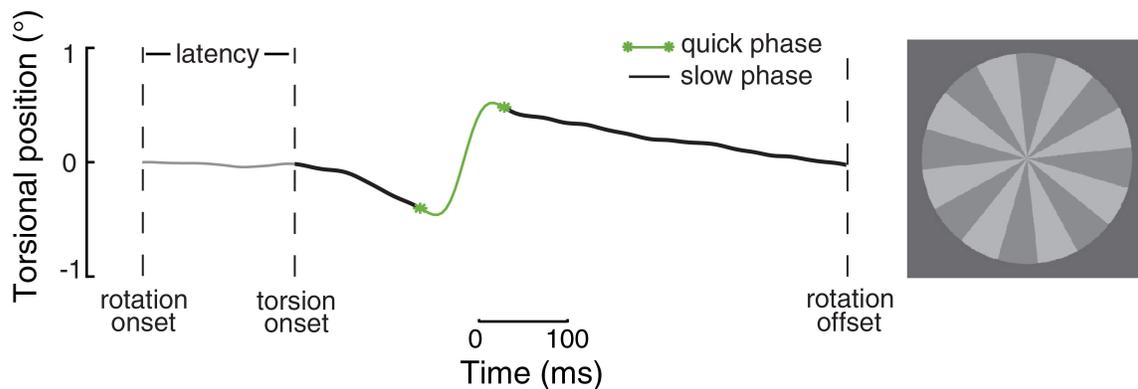
To have a clear vision of an object, we have to position its image on the tiny area near the centre of our retina, the fovea, where the density of photoreceptors is the highest (Curcio et al., 1990; Jacobs, 1979). As a result, two major functions of our eye movements are (1) shifting gaze to examine new objects in the environment, and (2) stabilizing gaze so that the image of the current object of interest can be kept on the fovea (Leigh and Zee, 2015). In the dissertation, I focus on two types of eye movements in response to visual motion, visually-induced torsion and smooth pursuit. Torsion serves to stabilize gaze in response to rotational motion. Smooth pursuit aims to keep the image of the current object of interest on the fovea, by rotating the eyes to closely follow the moving object.

### 1.2.1 Characteristics of torsion

Torsional eye movements are the rotations of the eyes about the line of sight (naso-occipital axis for primates), which refers to the third rotational direction of the eyes in addition to the translational (horizontal and vertical) directions. Torsion is mostly known as part of the vestibulo-ocular-reflex (VOR) in response to head/body rotation or static tilt. VOR is the compensatory eye rotation to head movements, and inputs to VOR are provided by the vestibular system, including the semicircular canals and otolith organs (Leigh and Zee, 2015). It serves to counteract the retinal image shift induced by self-motion. Torsional offsets on the retina also exist with eye rotation to oblique positions. These eye rotations follow Listing's law, and require no mechanical torsion ("false torsion"). According to Listing's law (von Helmholtz, 1867) and Donders' Law (Donders, 1848), for a given eye position, the way how the eye orients on the horizontal, vertical, and torsional directions are fixed (e.g., Enright 1986; Ferman et al. 1987; Haslwanter 1995; Haustein 1989; Tweed and Vilis 1990; for a review, see Klier et al. 2013). Assume that the eye rotates from a primary position (close to when looking straight ahead) to any given positions, the rotation axes of all such rotations lie in a single plane (Listing's plane). In other words, the eye orientation for a given position is only decided by the horizontal and vertical gaze directions. During movements from one eye orientation to another, the rotation vector will temporarily tilt away from Listing's plane, following the half-angle rule (Tweed and Vilis, 1987). In summary, torsional offsets on the retina accompany almost every gaze shift, and mechanical torsion occurs when Listing's plane is changed and the rotational vector of the eyes lies outside of Listing's plane, such as during head/body rotations.

In addition to head/body rotations, torsional eye movements can also be triggered by visual inputs. For example, torsional optokinetic nystagmus (OKN), or its early component named torsional ocular following response (OFR), occurs when observers view large-field rotating gratings (Farooq et al., 2004; Ibbotson et al., 2005; Sheliga et al., 2009). OKN/OFR mainly serves to stabilize the retinal image during sustained self-motion, supplementing VOR which mainly responds to the acceleration of self-motion (Leigh and Zee, 2015). Therefore, OKN/OFR responds to large-field vision motion which represents the shift of the world around us, and has a short latency (usually within 100 ms). Torsional OKN consists of two alternating phases

(Fig. 1.1): slow-phase rotations in the direction of visual motion, and quick-phase rapid reverse saccades resetting eye positions. Note that the torsional quick phases are different from the voluntary saccades that aim to bring the image of the object of interest onto the fovea. Torsional eye movements also occur along with smooth pursuit, when observers track translating and rotating patterns (Edinger et al., 2017). The latency and velocity of visually-induced torsion are modulated by visual stimulus properties such as size and rotational speed (Farooq et al., 2004; Ibbotson et al., 2005; Sheliga et al., 2009). In general, torsional velocity increases with the increase of stimulus size and rotational speed up to about  $200^\circ/\text{s}$ , and decreases when the rotational speed keeps increasing (Farooq et al., 2004; Sheliga et al., 2009). Torsional velocity gain, i.e., the ratio between eye and target velocity, is very small, usually below 0.1 (Farooq et al., 2004; Ibbotson et al., 2005; Sheliga et al., 2009).



**Figure 1.1:** Example trace of torsional eye positions in one trial from the study in Chapter 2.1. The torsional position of zero indicates the resting eye position. Positive values indicate torsional rotation in the clockwise direction. The visual stimulus is a rotating grating with a diameter of  $23.6^\circ$  (shown on the right), and a rotational velocity of  $25^\circ/\text{s}$  counterclockwise. The stimulus has rotated about  $19^\circ$  during the shown period. However, the magnitude and velocity of torsional eye movements are very small. The average torsional velocity in the slow phase in this trial is  $1.69^\circ/\text{s}$ .

### 1.2.2 Characteristics of smooth pursuit

Smooth pursuit eye movements are slow, continuous rotations of the eyes that allow close tracking of moving objects. These eye movements keep the retinal representation of a moving target close to the fovea, the area of the retina with the highest visual acuity (Curcio et al., 1990; Jacobs, 1979). A typical visual target used in the lab to elicit smooth pursuit is a single dot translating across the screen. Smooth pursuit also follows the average motion of a larger stimulus, such as a group of moving dots (Heinen and Watamaniuk, 1998). In addition to physical visual motion, pursuit can follow perceived motion, such as the apparent motion of an occluded object (Beutter and Stone, 2000; Ilg, 2008; Steinbach, 1976; Stone et al., 2000), or the illusory motion of either static stimuli (Braun et al., 2006) or non-existing motion paths (Maechler et al., 2021). However, pursuit cannot usually be elicited by purely imaginary motion (Lisberger et al. 1987; but see

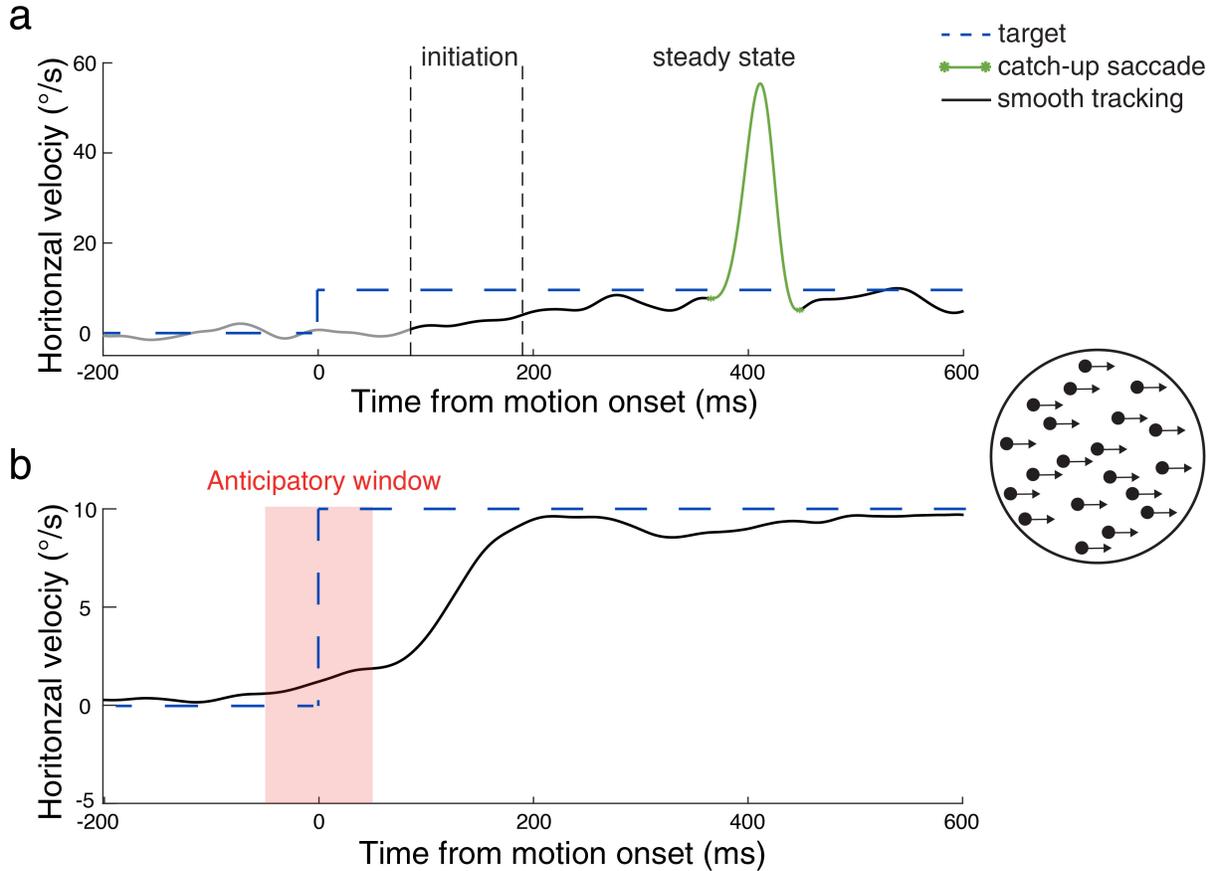
Lorenceanu 2012) or by non-visual motion stimuli (Berryhill et al., 2006). Pursuit in such cases will mostly consist of consecutive saccades rather than smooth tracking.

In addition, prediction is an intrinsic part of smooth pursuit control (Kowler et al., 2019). When tracking stimuli with periodic (e.g., sinusoidal) motion, the eyes soon have no lag behind or even a slight lead ahead of the target, indicating the capability to foresee the predictable motion path (Barnes and Asselman, 1991; Collewijn and Tamminga, 1984; Kowler and Steinman, 1979; Westheimer, 1954). Prediction is also needed when visual input is temporarily interrupted. For example, a bird you are tracking flies behind a tree. In order to not lose the target, you need to estimate when and where it will move out of the tree, and catch up with its motion as soon as possible once it reappears. During the temporary target occlusion, shortly before the expected reappearance of the target, the eyes will accelerate in preparation for the upcoming target motion, named predictive pursuit (Bennett and Barnes, 2004). Predictive pursuit is only observed if the target is expected to reappear (Barnes and Collins, 2008). Its velocity scales with the acceleration of the target (Bennett and Barnes, 2006; Bennett et al., 2007), indicating effective usage of cognitive and visual signals over time for the prediction of future motion. Smooth pursuit can also be purely driven by expectation before the appearance of any visual motion, named anticipatory pursuit. Such anticipatory pursuit can be elicited by repetition of visual motion or explicit cognitive cues indicating the upcoming motion direction (Jarrett and Barnes, 2001, 2002; Kowler, 1989; Santos et al., 2012; Santos and Kowler, 2017). Anticipatory pursuit reflects the representation of expectation in the visuomotor system.

Examples of smooth pursuit eye velocity traces are shown in Figure 1.2. The usual latency of human smooth pursuit is 100-150 ms (Carl and Gellman, 1987). Smooth pursuit usually consists of two phases with different processing mechanisms (Fig. 1.2a, without anticipatory pursuit): the initiation phase (up to about 100 ms after pursuit onset), also referred to as the open-loop, during which pursuit is fully dependent on retinal motion signals; the steady-state phase, also referred to as the closed loop, during which pursuit is mainly controlled by extraretinal signals—the non-visual signals related to the ongoing eye movements such as the feedback of motor commands (Lisberger, 2015). Pursuit properties during the initiation phase is usually measured by acceleration, which shows how fast the eye is catching up with the target. Pursuit during steady-state is usually described by velocity gain, which indicates how well the eye is keeping up with the target. Anticipatory pursuit is usually analyzed in the time window of  $\pm 50$  ms around target onset (Fig. 1.2b), when visual inputs cannot yet have an effect on the movement.

The smooth and continuous tracking component of pursuit is supplemented by catch-up saccades (Fig. 1.2a), which redirect the eye back onto the target once the spatial error is large enough (de Brouwer et al., 2002a,b). Catch-up saccades during smooth pursuit play a more dynamic role than the reverse saccades (quick phases) during torsion. The smooth tracking movements and the rapid redirecting movements of the eyes are mediated by different signals. Specifically, pursuit mainly responds to velocity errors, whereas saccades are primarily driven by position errors (Engel et al., 1999; Tarnutzer et al., 2007). This is consistent with their different functional demands of either keeping up with target motion, or quickly shifting gaze onto the target. However, pursuit and saccade share attentional resources (Jin et al., 2013) and decision signals

in target selection (Case and Ferrera, 2007; Heinen et al., 2018; Liston and Krauzlis, 2005; Srihasam et al., 2009), indicating coordination during visual orienting. Together with the findings of overlapping neural pathways (Krauzlis, 2005), pursuit and saccade can be considered as two effectors of one sensorimotor system aiming for optimal tracking (de Xivry and Lefèvre, 2007; Goettker and Gegenfurtner, 2021).



**Figure 1.2:** Example traces of smooth pursuit eye velocity. Eye velocity traces are from the study in Chapter 4, in response to a group of dots moving behind a static aperture to the right at the speed of  $10^\circ/\text{s}$  (shown on the right, the arrows are for illustration purposes). Blue dashed lines indicate target velocity. (a) A typical smooth pursuit velocity trace with catch-up saccades, consisting of the initiation phase during which the eyes are accelerating to catch up with the target, and then the steady-state phase during which the eyes closely track the target. (b) With expectation of future motion, anticipatory pursuit can be seen even before the visual motion onset. In both panels, positive velocity values indicate rightward motion. Note that the trace in (a) is from one trial, whereas the trace in (b) is averaged across trials (with saccades excluded) from one condition of one observer, as anticipatory smooth pursuit is usually small, and more visible in averaged velocity traces.

## 1.3 Relationship between perception and eye movements

Two questions elucidate on the relationship between perception and eye movements: Whether they share the same processing signals, and how they interact. The former question is usually examined by how similarly both systems respond to the same stimuli, and if the responses are correlated. The latter question could be addressed by examining the effects of one on the other. Below, I will summarize what we have already known about the relationship between perception and torsion/smooth pursuit, and how I am going to extend the existing knowledge. Briefly, depending on the amount of current evidence available, I will either start with the fundamental investigation on the existence of a link, or advance with more complex situations to understand to what extent the two systems are related. The complexity could either be in the stimuli itself, e.g., multiple motion signals across space, or in the processing of information over time, related to expectation and anticipatory eye movements.

### 1.3.1 Perception and Torsion

We have limited knowledge about the relationship between perception and torsion. It is very often ignored for at least two reasons. First, the small magnitude and velocity gain of torsion make the effect of torsion seemingly negligible. Second, torsion is often considered as a byproduct of eye movements due to Listing's law. However, studies have shown that changes in torsional eye position have an effect on perception (Haustein and Mittelstaedt, 1990; Murdison et al., 2019; Nakayama and Balliet, 1977; Wade and Curthoys, 1997). Regardless of whether the torsional eye position change was induced by oblique eye position in accordance to Listing's law (Haustein and Mittelstaedt, 1990; Murdison et al., 2019; Nakayama and Balliet, 1977), or by vestibular stimuli such as whole-body rotations (Wade and Curthoys, 1997), observers' perception of object orientation was biased against the torsional direction, indicating compensation for torsion in perception. In addition, torsion induced by rotational motion does not follow Listing's law (Angelaki et al., 2003; Crawford et al., 2003; Klier et al., 2013; Misslisch and Hess, 2000; Misslisch et al., 1994; Tian et al., 2007; Walker et al., 2004). The relationship between perception and visually-induced torsion is unclear. However, as visually-induced torsion is modulated by visual stimulus properties (Farooq et al., 2004; Ibbotson et al., 2005; Sheliga et al., 2009), a potential link in visual motion processing might exist between perception and torsion. I will examine this in Chapter 2.1.

It also remains unclear whether torsion is under cognitive control. For example, does anticipatory torsion exist, and is it under similar cognitive control as anticipatory pursuit? Despite the seemingly reflexive nature of torsion, some people can voluntarily induce torsion after training (Balliet and Nakayama, 1978). Attention has also been suggested to modulate torsion, as torsion seemed to be induced by attending to tilted words (Pashler et al., 2006), and would follow the attended stimulus instead of a simultaneously presented unattended stimulus (Stevenson et al., 2016). Such evidence suggests potential cognitive control behind torsional eye movements under certain circumstances. In Chapter 2.2, I will examine whether and how anticipatory torsion can be induced.

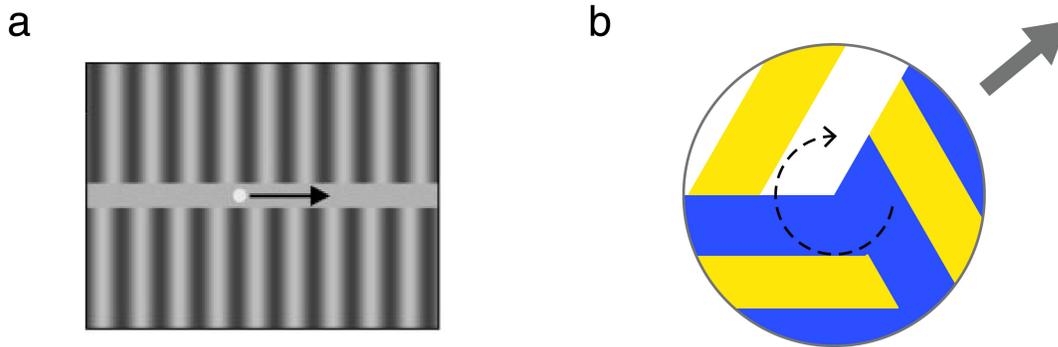
### 1.3.2 Perception and smooth pursuit

Unlike torsion, the close link between smooth pursuit and perception is well established (for reviews, see Schütz et al., 2011; Spering and Montagnini, 2011). Perception and pursuit show similar accuracy (how well the responses match the actual stimuli) and precision (how variable they are) in motion discrimination tasks (Gegenfurtner et al., 2003; Osborne et al., 2005; Stone and Krauzlis, 2003; Watamaniuk and Heinen, 1999). They also have similar temporal dynamics in motion discrimination tasks (Born et al., 2010; Lorenceau et al., 1993; Masson and Stone, 2002; Mukherjee et al., 2015; Osborne et al., 2007). This is potentially because both systems rely on motion processing in areas MT/MST (see section 1.4). Some findings even suggest that motion perception and smooth pursuit largely share the neural noises, indicating dependence on the same MT neurons for motion processing (Mukherjee et al., 2015; Osborne et al., 2007, 2005; Stone and Krauzlis, 2003), although results from other studies disagree (Gegenfurtner et al., 2003; Rasche and Gegenfurtner, 2009). Regarding their interaction, pursuit can be elicited by perceived/illusory motion (Beutter and Stone, 2000; Braun et al., 2006; Ilg, 2008; Maechler et al., 2021; Steinbach, 1976; Stone et al., 2000), as mentioned in Section 1.2.2. Perception is affected by pursuit with both impairments and enhancements. For example, objects appear to move slower during pursuit than fixation (Turano and Heidenreich, 1999). The motion direction of the pursuit target seems to be repelled away from the pursuit trajectory (Morvan and Wexler, 2009; Souman et al., 2005), potentially due to imperfect compensation of the eye-movement-induced retinal motion. In contrast, extraretinal signals of eye movements can provide additional information about the object motion, and enhance prediction of motion direction (Spering et al., 2011b).

Despite the close link between perception and pursuit, dissociations between perceptual and pursuit responses in the same task suggest that signal processing for perception and pursuit might separate at some point (Spering and Carrasco, 2015). For example, perception is less sensitive to acceleration signals than pursuit (Bennett and Benguigui, 2013; Tavassoli and Ringach, 2010), and pursuit direction is affected by the motion of stimuli that we are unaware of (Spering et al., 2011a). The questions that follow are when and where the two systems may separate. To better understand the control of both systems and what functional purposes they serve, we need comparisons between perception and pursuit under different task situations. To further this understanding, I will examine how perception and pursuit process motion signals across different spatial and temporal scales, representing different types of common situations in daily life.

By motion signals across different spatial scales, I refer to visual stimuli that are more complex than a small target translating across a blank screen, which is the typical visual stimulus for studying smooth pursuit. In our daily visual environments, objects move in front of complex visual backgrounds, which create large field retinal motion on our retina that is against the target motion direction (Fig. 1.3a). A challenge for both perception and pursuit is how to process the local target motion vs. the global background motion. Different strategies have been suggested to be used by perception and pursuit. Whereas perception followed the relative difference between target and background speed, pursuit velocity followed the averaged velocity of target and background motion (Spering and Gegenfurtner, 2007b). In addition to different spatial scales of target and background, the target itself can also contain motion signals that occur on different spatial

scales, such as motion of the whole object and components within the object. For example, whereas a flying volleyball has a curvature motion trajectory above our head, its texture also presents a rotational motion within the ball (Fig. 1.3b). How perception and pursuit process object vs. internal motion is unclear, as both associations (Beutter and Stone, 2000; Stone et al., 2000) and dissociations (Hughes, 2018) have been shown. In Chapter 3, I will investigate this question by examining how perception and pursuit of object motion are affected by internal motion.



**Figure 1.3:** Examples of motion signals on different spatial scales. (a) A single dot target surrounded by large-scale textured background, adapted from Fig. 1 in Spering and Gegenfurtner (2007a). Both the target and background are moving horizontally, presenting local (target) and global (background) motion at the same time. (b) A flying and rotating volleyball with both object motion and internal motion. The grey solid arrow indicates the object motion which operates on a larger spatial scale. Black dashed arrows indicate the additional internal motion within each object, which is different from the object motion and operates on a smaller spatial scale.

In addition to visual stimuli across spatial scales, we also process motion signals presented across time. We not only encode current visual motion signals, but also make use of past experience. How often a stimulus is seen will shape expectation about future motion (de Lange et al., 2018; Seriès and Seitz, 2013). When a certain motion direction appears more frequently, our perception can be biased towards the same direction in upcoming ambiguous stimulus displays (Chalk et al., 2010). Expectation based on past experience modulates visually-driven pursuit (Darlington et al., 2018; Deravet et al., 2018) and drives anticipatory pursuit in the expected direction (Kowler, 1989; Santos and Kowler, 2017). However, results from studies directly comparing effects of expectation on perception and pursuit are inconclusive. When induced by cognitive cues, expectation results in similar biases in direction perception and steady-state pursuit—both follow the expected direction (Krauzlis and Adler, 2001). When expectation is based on recent trial history, anticipatory pursuit velocity increases if faster stimuli were presented in recent trials, but a slower speed is perceived after the same trials (Maus et al., 2015). In the natural environment, we do not always have explicit cues. Our inference about the world based on general probabilities of events in the environment (Chalk et al., 2010) might be different from the inference based on short-term fluctuations of recent history (Chopin and Mamassian, 2012; Fritsche et al., 2020). In Chapter 4, I will examine whether expectation based on a general

inference of the environment modulates perception and pursuit similarly.

## **1.4 Neural correlates of motion perception and eye movements**

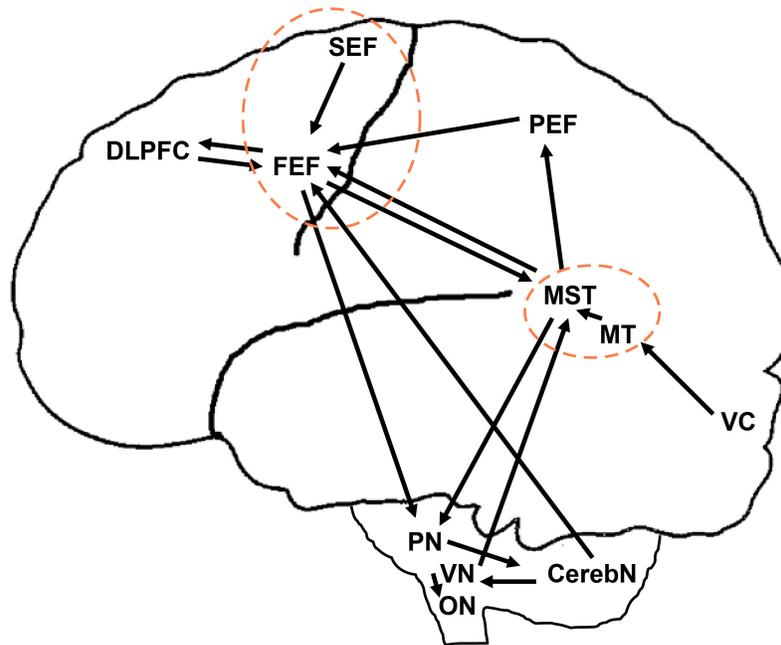
In this section, I will start with an overview of the neural pathways for smooth pursuit and torsion insofar as they are relevant for this dissertation. I will then review cortical areas for a potential link between perception and eye movements in more detail. Specifically, because I manipulated visual motion and expectation signals in this dissertation, I will focus on cortical areas related to the processing of visual motion and anticipatory signals. Behavioural associations/dissociations from studies presented in this dissertation could contribute to our knowledge of how perception and pursuit/torsion might be controlled by these areas.

### **1.4.1 Neural pathways for smooth pursuit and torsion**

Neural pathways for smooth pursuit eye movements have been studied extensively in macaque monkeys (for reviews, see Krauzlis 2004, 2005; Leigh and Zee 2015; Lencer and Trillenber 2008; Lisberger 2010, 2015; Thier and Ilg 2005). Corresponding cortical areas in the human brain have been revealed by neuroimaging studies (e.g., Dieterich et al., 2009; Kimmig et al., 2008; Konen and Kastner, 2008; Petit and Haxby, 1999; Watson et al., 1993; Zeki et al., 1991) and by patient studies (e.g., Barton and Sharpe, 1998; Barton et al., 1996; Braun et al., 1996; Lekwuwa and Barnes, 1996a,b; Pierrot-Deseilligny, 1994; Rivaud et al., 1994).

Visual input is first transmitted from the retina via the LGN to area V1, then projected to MT/MST (V5/MT+ in the human; Dieterich et al. 2009; Kimmig et al. 2008; Petit and Haxby 1999; Watson et al. 1993; Zeki et al. 1991; see Fig. 1.4). Areas MT/MST are related to the processing of visual motion signals for smooth pursuit eye movements (Chukoskie and Movshon, 2009; Ilg, 2008; Krauzlis, 2004; Lisberger, 2010; Lisberger and Movshon, 1999). Signals are further processed in parietal and frontal cortical areas. The posterior parietal cortex, including lateral and ventral intraparietal areas (parietal eye fields in the human; Dieterich et al. 2009; Kimmig et al. 2008; Konen and Kastner 2008; Petit and Haxby 1999), is responsible for attentional modulation and target selection for smooth pursuit (Krauzlis, 2004; Leigh and Zee, 2015; Lencer and Trillenber, 2008). The frontal eye fields (FEF) integrate visual and non-visual (e.g., extraretinal and predictive) signals (Bakst et al., 2017; Nuding et al., 2009; Tanaka and Lisberger, 2001) and generate oculomotor commands for smooth pursuit (Gottlieb et al., 1993, 1994). FEF has connections to the supplementary eye field (SEF) and the dorsal lateral prefrontal cortex (Ding et al., 2009; Tian and Lynch, 1996). SEF is related to the planning of smooth pursuit and the control of anticipatory pursuit (de Hemptinne et al., 2008; Fukushima et al., 2013; Heinen et al., 2011; Missal and Heinen, 2001, 2004). The dorsal lateral prefrontal cortex is related to working memory and learning during smooth pursuit (Burke and Barnes, 2008; Lencer and Trillenber, 2008; Nagel et al., 2006; Pierrot-Deseilligny et al., 2004). Neurons in areas MT/MST and FEF project to the pontine nuclei (dorsolateral pontine nuclei, DLPN; the nucleus reticularis tegmenti pontis, NRTP), where both visual motion and eye movement signals are encoded (Mustari et al., 2009; Ono et al., 2005). Information is then projected via the cerebellum (the flocculus, paraflocculus, and

vermis) to the vestibular nuclei and eventually the oculomotor nuclei, where motor commands for smooth pursuit are refined and generated (Krauzlis, 2004; Leigh and Zee, 2015; Lencer and Trillenber, 2008).



**Figure 1.4:** Hypothetical scheme for the smooth pursuit network in the human brain. MT/MST and frontal cortical areas (FEF and SEF) are highlighted by orange dashed circles, as they are the major sites relevant for the relationship between perception and eye movements examined in this dissertation. Arrows indicate anatomical connections between areas. VC = primary visual cortex; MT = middle temporal area; MST = medial superior temporal area; PEF = parietal eye fields; FEF = frontal eye field; SEF = supplementary eye field; DLPFC = dorsolateral prefrontal cortex; PO = pontine nuclei; VN = vestibular nuclei; CerebN = cerebellar nuclei; ON = oculomotor nuclei. Modified from Figure 5 in Lencer and Trillenber (2008).

For neural pathways of torsion, subcortical areas are better known than cortical areas. Torsional quick phases are generated by activities of the burst neurons in the rostral interstitial nucleus of the medial longitudinal fasciculus (riMLF) in the brainstem (Moschovakis et al., 1991a,b; Suzuki et al., 1995). riMLF has reciprocal connections with the interstitial nucleus of Cajal (INC; Horn 2006). INC integrates velocity-coded commands to generate torsional eye position signals, and contributes to slow-phase torsional rotations (Crawford et al. 1991; Helmchen et al. 1998; for reviews, see Klier et al. 2013; Leigh and Zee 2015). Both riMLF and INC project to oculomotor neurons (cranial nerves III, IV, and VI) that drive the eye muscles controlling vertical and torsional rotations (Horn et al., 2003; Kokkoroyannis et al., 1996; Moschovakis et al., 1991a,b). riMLF and INC receive inputs from the vestibular nuclei (Horn, 2006; Kokkoroyannis et al., 1996). The upstream cortical areas contributing to the control of ocular torsion remain unclear (Crawford et al., 2003; Klier et al., 2013). However, as torsion has been shown to be an integral part of smooth pursuit

(Edinger et al., 2017) and OKN/OFR (Farooq et al., 2004; Ibbotson et al., 2005; Sheliga et al., 2009), it might be controlled by similar neural pathways. Neurons in MST are sensitive to visual rotational motion (Graziano et al., 1994; Mineault et al., 2012; Tanaka et al., 1989), and play a role in smooth pursuit (Mustari et al., 2009; Ono et al., 2005) as well as OKN/OFR (Dürsteler and Wurtz, 1988; Kawano et al., 1994; Take-mura and Kawano, 2002). MST projects to DLPN (Boussaoud et al., 1992; Distler et al., 2002; Hoffmann et al., 2009; Ono et al., 2005; Ono and Mustari, 2009), from where eye movement signals are relayed to the cerebellum and then reach the vestibular nuclei. MST also projects to FEF (Churchland and Lisberger, 2005), which then projects to riMLF (Lynch and Tian, 2006; Yan et al., 2001) and NRTP (Mustari et al., 2009; Ono et al., 2005; Ono and Mustari, 2009; Suzuki et al., 1999). NRTP contributes to the correction of torsional errors during saccades (Van Opstal et al., 1996). In addition, MST projects to the pontine nuclei via the accessory optic system and the nucleus of the optic tract (NOT; Buttner-Ennever et al. 1996). NOT is crucial in the generation of OKN, especially the slow phases (Cohen et al., 1992; Kato et al., 1988; Masseck and Hoffmann, 2009). In summary, MST might be the cortical area related to the processing of visual rotational motion for visually-induced torsion, although such a connection still needs to be confirmed.

#### **1.4.2 Cortical areas for the perception-eye movement link**

Connections between the smooth tracking eye movements and perception likely occur in cortical areas, where the processing of visual motion signals and their integration with non-visual (e.g., extraretinal and anticipatory) signals are carried out to form a representation of object motion for perception, or for the guidance of eye movements. Below, I will introduce the major cortical areas for smooth pursuit eye movements in more detail and discuss how the same areas mediate perception. Among the cortical areas, two groups of areas (highlighted in Fig. 1.4) are particularly relevant to studies presented in the dissertation: MT/MST, from where motion processing signals could be shared between perception and eye movements; FEF/SEF, where anticipatory smooth pursuit are controlled based on expectation, and top-down modulations based on expectation might be generated to affect perception.

##### **Cortical areas MT/MST process visual motion signals for perception and eye movements**

MT neurons receive input mainly from early visual areas (mostly V1, but also V2 and V3) and are tuned to visual motion direction and speed (Maunsell and Van Essen, 1983a,b; Van Essen et al., 1981). Whereas V1 neurons detect simple visual motion, MT neurons have larger receptive fields and pool inputs from V1 (Dubner and Zeki, 1971), thus can further process visual motion signals of complex patterns. For example, when two gratings moving in different directions are superimposed, observers usually perceive a coherent plaid pattern which moves in a global motion direction different from the direction of either the component grating (Adelson and Movshon, 1982). Some MT neurons respond to the motion of a component grating, whereas some MT neurons respond to the global motion of the pattern (Movshon and Newsome, 1996; Rust et al., 2006). In addition, MT neurons have two types of center-surround receptive fields. Neurons with excitatory center-surround receptive fields respond well to large-field, global motion signals, whereas neurons

with inhibitory center-surround receptive fields respond well to small-scale, local motion signals (Allman et al., 1985; Born, 2000; Born and Tootell, 1992; Tanaka et al., 1986). Different types of center-surround receptive fields allow MT neurons to integrate and segregate motion signals (Born and Bradley, 2005). MT also receives direct inputs from LGN bypassing V1 (Atapour et al., 2022; Bridge et al., 2008; Gaglianese et al., 2012; Nassi and Callaway, 2009; Sincich et al., 2004), or from the retina-superior colliculus-pulvinar pathway bypassing LGN and V1 (Berman and Wurtz, 2010, 2011).

MT neural activities correspond to the temporal dynamics of motion representation for perception (Born et al., 2010) and pursuit (Born et al., 2006; Lisberger and Movshon, 1999; Pack and Born, 2001). Lesions in MT selectively impair motion perception (Cooper et al., 2012; Hess et al., 1989; Newsome and Paré, 1988; Shipp et al., 1994). Activities of MT neurons are correlated with the sensitivity and reaction time of perceptual choices in direction discrimination tasks (Britten et al., 1996, 1992; Cohen and Newsome, 2008, 2009). Lesions in MT also impair the generation of smooth pursuit (Newsome et al., 1985; Thurston et al., 1988). Microstimulation of MT neurons modulates the speed and direction of ongoing pursuit, and even generates pursuit when the target is stationary (Groh et al., 1997). To sum up, MT provides visual motion processing signals for both perception and pursuit. However, subcortical pathways from the retina to MT bypassing V1 might be related to dissociations between perception and eye movements (Spering and Carrasco, 2015). The retinocollicular (retina-superior colliculus-pulvinar-MT) and/or geniculo-extrastriate (retina-LGN-MT) projections might provide rapid processing of visual signals for eye movements without them reaching perceptual awareness.

MST receives direct input from MT (Ungerleider and Desimone, 1986), and has two subregions that play slightly different roles in visual motion processing: the lateral (MSTl) and the dorsal portion (MSTd). Neurons in MSTl respond to small moving spots (Komatsu and Wurtz, 1989). Microstimulation of them accelerates ongoing pursuit (Komatsu and Wurtz, 1989). Some MSTl neurons encode target motion in world-centered coordinates during smooth pursuit (Ilg et al., 2004). Neurons in MSTd respond well to large-field motion patterns relevant to heading direction, including rotation, expansion, and contraction (Duffy and Wurtz, 1997; Geesaman and Andersen, 1996; Kawano et al., 1994; Saito et al., 1986), and encode signals in head-centered coordinates during smooth pursuit (Fujiwara et al., 2011). Because MST responds well to optic flow stimuli, it contributes to heading perception (Andersen et al., 2000; Britten and Van Wezel, 2002) and to reflexive tracking responses, such as OKN and OFR (Dürsteler and Wurtz, 1988; Takemura and Kawano, 2006; Takemura et al., 2007). As mentioned in the section above, because neurons in MSTd are sensitive to rotational motion (Graziano et al., 1994; Mineault et al., 2012; Tanaka et al., 1989), they might also play a role in the control of visually-induced torsion. Unlike MT, which only responds to retinal motion, MST also shows activity in the absence of visual motion during smooth pursuit, indicating extraretinal inputs (Newsome et al., 1988). Therefore, MST is not only related to visual motion processing (Celebrini and Newsome, 1994, 1995; Kregelberg et al., 2003; Rudolph and Pasternak, 1999), but also plays a role in cancelling the retinal motion induced by eye movements to help derive the veridical object motion in the world (Bradley et al., 1996; Haarmeier et al., 1997; Inaba et al., 2011, 2007).

## **Frontal cortical areas integrate visual and non-visual signals and contribute to anticipatory smooth pursuit control**

Area FEF is directly related to the generation of oculomotor commands for smooth pursuit. FEF neurons are activated before and during pursuit in their preferred direction (Gottlieb et al., 1994). Microstimulation of FEF neurons evokes smooth pursuit even during attempted fixation (Gottlieb et al., 1993, 1994). During smooth pursuit, FEF integrates a variety of signals, including eye velocity (Bakst et al., 2017; Fukushima et al., 2000; Gottlieb et al., 1994), eye acceleration (Bakst et al., 2017; Ono and Mustari, 2009; Tanaka and Fukushima, 1998), retinal image motion (Bakst et al., 2017; Fukushima et al., 2000), and past experience (Darlington et al., 2018; Yang et al., 2012). In addition, FEF neurons are crucial for updating the internal representation of visual motion information, thereby enabling predictive pursuit in response to periodic motion or temporary target occlusion (Barborica and Ferrera, 2002; Fukushima et al., 2002; Schoppik et al., 2008). Inactivation of FEF almost eliminates pursuit in the preferred direction (Shi et al., 1998), and impairs predictive pursuit during sinusoidal tracking (Braun et al., 1996; Heide et al., 1996; Keating, 1991; Macavoy et al., 1991; Morrow and Sharpe, 1995). FEF also contributes to anticipatory pursuit. FEF activities in preparation for smooth pursuit could start more than 600 ms before target onset (Darlington and Lisberger, 2020), indicating a potential role in the control of anticipatory pursuit. Lesions in FEF impair anticipatory pursuit (Macavoy et al., 1991).

Area SEF is adjacent to FEF and related to the planning of smooth pursuit, rather than the actual movement. When a decision has to be made to determine whether to perform smooth pursuit or not, activities of SEF neurons reflect interpretation of the decision rules for smooth pursuit but not the execution of the oculomotor decision (Heinen et al., 2011; Yang and Heinen, 2014; Yang et al., 2010). In addition, SEF plays a critical role in anticipatory pursuit. SEF neurons are more activated when target motion is predictable than when it is unpredictable, and their peak activities shift with the duration of target events (Heinen and Liu, 1997). SEF stimulation increases the velocity and decreases the latency of anticipatory pursuit to motion targets that are predictable in the onset time, speed, and direction (Missal and Heinen, 2004). When direction expectation is induced by a color cue, SEF activities encode the expected future motion direction and the direction of subsequent anticipatory pursuit (de Hemptinne et al., 2008).

Frontal areas might affect perception by top-down modulations. FEF projects to MT (Ruff et al., 2008; Silvanto et al., 2006), and SEF outputs could also reach MT via FEF (Ninomiya et al., 2012). FEF modulates visual attention oriented by symbolic cues and affects detection of visual stimulus presented at the attended location (Chanes et al., 2012; Chica et al., 2014; Taylor et al., 2007). Therefore, FEF might affect motion perception when expectation is induced by cognitive cues. It remains unclear whether FEF also encodes expectation based on history. However, as FEF integrates current visual signals with past experience for smooth pursuit (Darlington et al., 2018; Yang et al., 2012), similar activities might also affect perception.

In summary, whereas the neural pathways for smooth pursuit and the subcortical pathways for torsion are well-known, cortical areas controlling torsion remain unclear. It is also not fully understood to what extent

perception and smooth pursuit share signal processing in visual areas MT/MST, or whether expectation signals are shared between perception and smooth pursuit. By examining the associations and dissociations between perception and eye movements under different stimulus and task conditions, we could get implications about the answers to these questions. In the next section, I will give an overview of the research objectives of the four experimental studies to be presented in this dissertation.

## **1.5 Dissertation overview**

The overarching goal of this dissertation is to better understand the perception-action link, by testing how both systems respond to signals across spatial and temporal scales. The main question to be addressed is to what extent perception and action share signal processing. To answer this question, I study how motion perception and eye movements process visual motion and expectation signals. I focus on two types of eye movements in response to visual motion, visually-guided torsion and smooth pursuit. These eye movements vary in the level of subcortical and cortical control and could have different degrees of connection with perception. Torsion is mostly controlled by subcortical pathways and more reflexive. I will examine whether torsion is related to motion perception, and how much it is under cognitive control. Smooth pursuit involves more signal processing in cortical areas and is more under voluntary control. It has already been shown to have a close link with motion perception (Schütz et al., 2011; Spering and Montagnini, 2011). I will examine how pursuit is related to perception under more complex situations, when multiple motion signals are presented across space, or when expectation based on past experience is manipulated. The results of these studies will further our understanding of the perception-action link about under what conditions perception and action are associated or dissociated, and provide insights about the underlying neural mechanisms.

### **Research objective of study 1 (Chapter 2.1)**

Based on indirect evidence suggesting a potential link between motion perception and torsion, I examine whether perception and torsion are related under a motion-induced illusion.

### **Research objective of study 2 (Chapter 2.2)**

To further explore how much torsion is under cognitive control, I investigate whether anticipatory torsion can be induced, and compare it with anticipatory pursuit, which is known to be elicited by history as well as different types of cognitive cues.

### **Research objective of study 3 (Chapter 3)**

Motion perception and smooth pursuit have a tight link, especially under simple motion conditions. I further examine how they process motion signals across different spatial scales (object vs. internal motion) under more complex situations.

### **Research objective of study 4 (Chapter 4)**

Finally, I study whether expectation based on past experience affect motion perception and anticipatory pursuit in the same way, and examine a few potential causes for their dissociation.

## Chapter 2

# Visually-induced torsion is linked to perception, but under limited cognitive control

We know little about whether and how torsion is related to perception, as torsion is often considered as a type of small-magnitude reflexive eye movements. However, several lines of evidence point to a potential link between perception and torsion. In the first study<sup>1</sup> (2.1), we examine whether perception and visually-induced torsion are correlated by utilizing a motion-induced illusion. In the second study (2.2), we further explore how much torsion is under cognitive control, by testing under what conditions anticipatory torsion can be induced.

## 2.1 Ocular torsion is related to perceived motion-induced position shifts

### 2.1.1 Introduction

Torsional eye movements are rotations of the eye about the line of sight that accompany almost every gaze shift (Ferman et al., 1987; Haustein, 1989; Lee et al., 2000; Straumann et al., 1996; Tweed et al., 1992; Tweed and Vilis, 1990). Torsion can also be driven by rotations of the head or whole body (Bockisch et al., 2003; Crawford et al., 2003; Misslisch and Hess, 2000; Misslisch et al., 1994) or by exposure to radial motion (Edinger et al., 2017; Farooq et al., 2004; Ibbotson et al., 2005; Sheliga et al., 2009). In humans, torsional eye movements are typically small and slow, with velocity gains commonly reported to be less than 0.1, and they are therefore usually disregarded in visual psychophysics and eye movement experiments.

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<sup>1</sup>A version of this study has been published as Wu, X. and Spering, M. (2019). Ocular torsion is related to perceived motion-induced position shifts. *Journal of Vision*, 19(12):1–13. Contents are almost identical except for: 1. Minor adjustments of Figure 2.3, 2.4, 2.6, and 2.7 (added 95% confidence intervals); 2. Additional explanation of the variables and factors in rmANOVA and the correlation analysis in Methods (“Hypotheses and statistical analysis”); 3. Additional explanation of neural correlates of torsion in Discussion (“Neural correlates of a torsion-perception link”).

However, some studies have shown that torsional eye position influences visual perception. For example, when asked to judge the orientation of a tilted line, observers' judgments were biased in the opposite direction of torsion, indicating that torsional eye position was taken into account during this task (Haustein and Mittelstaedt, 1990; Murdison et al., 2019; Nakayama and Balliet, 1977; Wade and Curthoys, 1997). In these studies, torsion was induced by moving the eyes to a tertiary (oblique) location (Haustein and Mittelstaedt, 1990; Murdison et al., 2019; Nakayama and Balliet, 1977) or by whole-body rotations (Wade and Curthoys, 1997). Oblique eye position-induced torsion is the by-product of eye rotations as described by Listing's law (Ferman et al., 1987; Haustein, 1989), and self-motion induced torsion is modulated by the vestibular system (Leigh and Zee, 2015). By contrast, visually-induced torsion—eye rotations that are triggered by viewing rotating visual objects may involve different mechanisms and cortical pathways. The relationship between this type of torsion and visual perception has not yet been studied. The goal of the present study is to investigate whether and how visually-induced torsion relates to visual motion perception.

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

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

Whereas saccades have frequently been linked to perceptual phenomena such as motion-induced illusions (e.g., Becker et al., 2009; de'Sperati and Baud-Bovy, 2008; Zimmermann et al., 2012), ocular torsion

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

## **2.1.2 Methods**

### **Observers**

We tested 15 observers (mean age  $25.4 \pm 7.5$  years, three males) in Experiment 1 and 10 observers (mean age  $24.3 \pm 5.5$  years, two males) in Experiment 2; all had normal visual acuity as per self-report. Observers had no history of ophthalmic, neurologic, or psychiatric disease. Experimental procedures followed the tenets of the Declaration of Helsinki and were approved by the University of British Columbia Behavioural Research Ethics Board. All observers participated after giving written informed consent and received \$15 CAD as compensation.

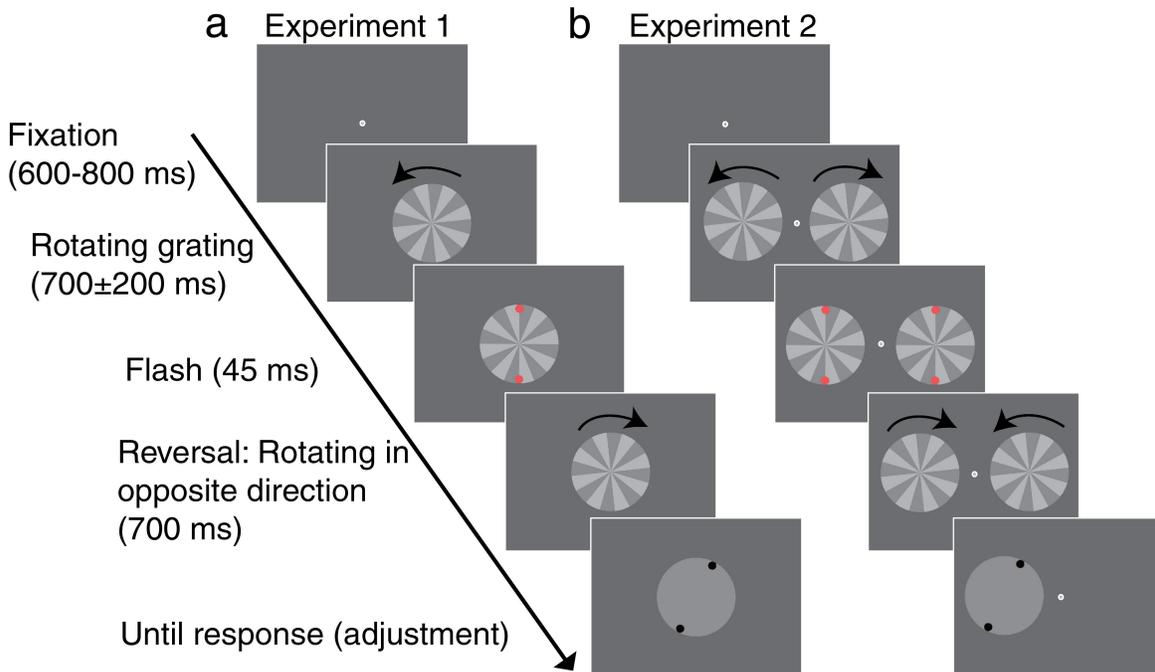
### **Setup**

Observers viewed stimuli in a dimly lit room on a gamma-corrected 19-in. CRT monitor set to a refresh rate of 85 Hz (ViewSonic Graphic Series G90fB,  $1,280 \times 1,024$  pixels,  $36.3 \times 27.2$  cm; ViewSonic, Brea, CA). The viewing distance was 37 cm in Experiment 1. The viewing distance in Experiment 2 was increased to 45 cm following initial reports that two oppositely rotating stimuli at close proximity caused dizziness. All stimuli were shown on a uniform dark grey background ( $17 \text{ cd/m}^2$ ). Each observer's head was stabilized using a chin rest. Stimuli and procedure were programmed in MATLAB Version R2015b (MathWorks, Natick, MA) and Psychtoolbox Version 3 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

### **Visual stimuli and procedure**

Figure 2.1 shows the timeline of one experimental trial for each experiment. The flash-grab effect was

triggered by presenting one rotating grating in the centre of the screen in Experiment 1 (Fig. 2.1a) or two gratings, each centred at an offset of  $10.5^\circ$  relative to the centre of the screen, in Experiment 2 (Fig. 2.1b). Each grating was an eight-cycle square-wave grating with Michelson contrast of 0.25 (average luminance  $50 \text{ cd/m}^2$ ). The grating in Experiment 1 was  $23.6^\circ$  in diameter and rotated at one of five speeds (25, 50, 100, 200,  $400^\circ/\text{s}$ ). The two gratings in Experiment 2 each had a diameter of  $20^\circ$ , rotating simultaneously at the same speed (25, 50, 100, or  $200^\circ/\text{s}$ ) but in opposite directions. In both experiments, each stimulus's rotational direction reversed from clockwise (CW) to counterclockwise (CCW) or vice versa. At the reversal of rotational direction, a flash stimulus (two red disks, each with a diameter of  $2.5^\circ$ , one shown at 12 o'clock, the other at 6 o'clock) was briefly superimposed on each grating for four frames ( $\sim 47 \text{ ms}$ ). The grating remained stationary while the flash was presented.



**Figure 2.1:** Trial timeline in (a) Experiment 1 and (b) Experiment 2. Rotating grating(s) were presented after a 600- to 800-ms fixation interval. Following a period of continuous motion in one direction for 500 to 900 ms, the flash was presented just before the grating's direction reversed. Each trial ended with the observer's response following the reference stimulus prompt. In Experiment 2, observers reported perception only on the side of the reference stimulus.

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

and observers were asked to estimate the perceived location of the flash on that side.

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

### Baseline tasks for perception and eye movements

To account for possible response bias during the perceptual reports, we conducted a baseline-perception block (60 trials) before experimental blocks. This block also served as a practice block for perceptual reports with the trackball mouse. In baseline-perception trials, observers reported the perceived location of a flash following the presentation of a stationary uniform grey disk (luminance  $50 \text{ cd/m}^2$ ); the timeline was identical to experimental trials. The flash was tilted away from vertical in either direction (CW or CCW) and presented at one of five angles ( $2, 4, 8, 12, 16^\circ$ ) in Experiment 1. In Experiment 2, the flash was shown at one of three angles ( $2, 8, \text{ or } 16^\circ$ ) but tilted in opposite directions on the left and right disk. Orientation of the flash was counterbalanced. Only perceptual judgments were analyzed in these trials and served as a response bias baseline for each observer’s perceptual judgments in experimental trials. We also included a baseline-torsion block, in which observers were asked to fixate in the screen centre and passively view a grating that rotated continuously for 1,800 to 2,200 ms. The gratings had the same properties as described for Experiments 1 and 2. The purpose of baseline torsion was to confirm that the rotating gratings successfully elicited visually-induced torsional eye rotations. After each trial, a reference stimulus was still presented, but no perceptual task was required. Only torsional eye movements were analyzed in these baseline trials.

### Perceptual data bias correction

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

$$A_{\text{physical}} = \begin{cases} \frac{A_{\text{perceived}} - b}{a}, & A_{\text{perceived}} < 16a + b \\ \frac{16 - b}{a}, & A_{\text{perceived}} \geq 16a + b \end{cases} \quad (2.1)$$

Here, we simply assumed that the response bias of a perceived angle larger than  $16^\circ$  remains the same

as the bias of  $16^\circ$ . Because the illusory position shift was mostly less than  $25^\circ$  in the current experiment, such an assumption might result in a conservative estimate of the response bias by underestimating the bias for angles larger than  $16^\circ$ .

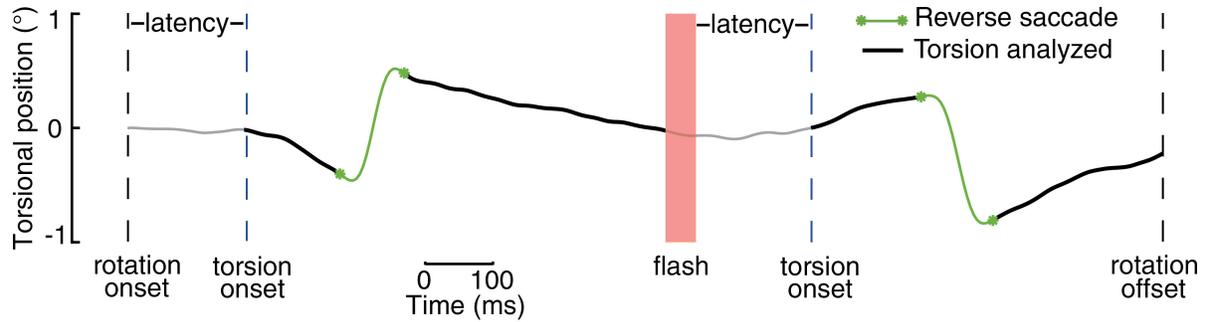
### **Eye movement recording and analysis**

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

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

Eye movements in experimental trials were analyzed in two time windows separated by the reversal of visual rotation (see Fig. 2.2): before reversal (initial torsion onset to flash onset) and after reversal (after-reversal torsion onset to rotation offset). Torsional velocity was calculated separately for each analysis interval shown in Figure 2.2. Because the magnitude of torsional rotations was small, torsion latency was

defined based on each individual observer’s mean torsional velocity trace for each rotational speed. For each analysis interval, the first point at which the mean torsional velocity exceeded  $0.1^\circ/\text{s}$  was defined as torsion onset. This analysis was conducted in a time interval from 80 ms after motion onset to motion offset, because the human torsional ocular following response, a fast reflexive response to large-field rotational motion, has a latency of  $\sim 80$  ms (Sheliga et al., 2009). In Experiment 2, torsional eye movements were not expected to follow a consistent motion direction. Therefore, we defined torsion onset as the mean torsion latency for each rotational speed from Experiment 1.



**Figure 2.2:** Example of torsional eye position in one experimental trial from Experiment 1. The visual rotation was initially CCW, then CW. Flash onset corresponds to the offset of before-reversal motion, and flash offset corresponds to the onset of after-reversal motion. Bolded black segments of the line indicate the saccade-free torsion phase that is included in the analysis of torsional velocity.

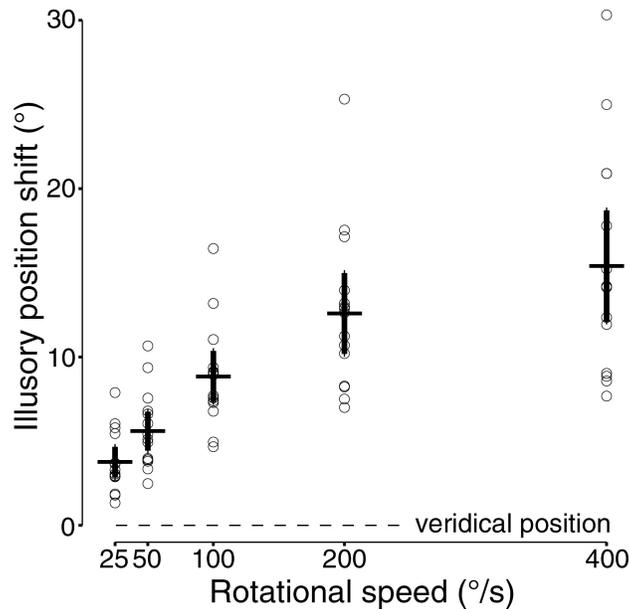
### Hypotheses and statistical analysis

In both experiments, we tested how perception and torsion responded to rotational motion and analyzed the relationship between the magnitude of the illusory position shift and torsional velocity. If perception and torsion share motion-processing inputs, they should be similarly affected by visual rotational speeds; that is, increases in the magnitude of the perceptual illusion with increasing rotational speed should be accompanied by increases in torsional velocity. Correspondingly, the strength of the perceptual illusion should be correlated with torsional velocity. To investigate these hypotheses, we used within-subjects repeated-measures analysis of variance (ANOVA) to examine effects of visual rotational speed on illusory position shift and torsional velocity. Illusory position shift or torsional velocity is the dependent variable, and *rotational speed* (Exp1: 25, 50, 100, 200, or  $400^\circ/\text{s}$ ; Exp2: 25, 50, 100, or  $200^\circ/\text{s}$ ) is the within-subjects factor. Effect sizes were reported as generalized eta-squared ( $\eta_g^2$ ) for all ANOVAs (Bakeman, 2005). Pearson’s correlations were calculated to assess the relationship between illusory position shift and torsional velocity across observers. Partial correlations were calculated with speed as a covariate. If perception and torsion were related, we would expect a significant correlation across observers. We did not examine the within-subject correlation on a trial-by-trial basis due to the small magnitude of torsional responses. Statistical analyses were conducted in R Version 3.5.1 (R Core Team 2019; package “ez,” Lawrence 2016; package “ppcor,” Kim 2015).

### 2.1.3 Results

#### Experiment 1

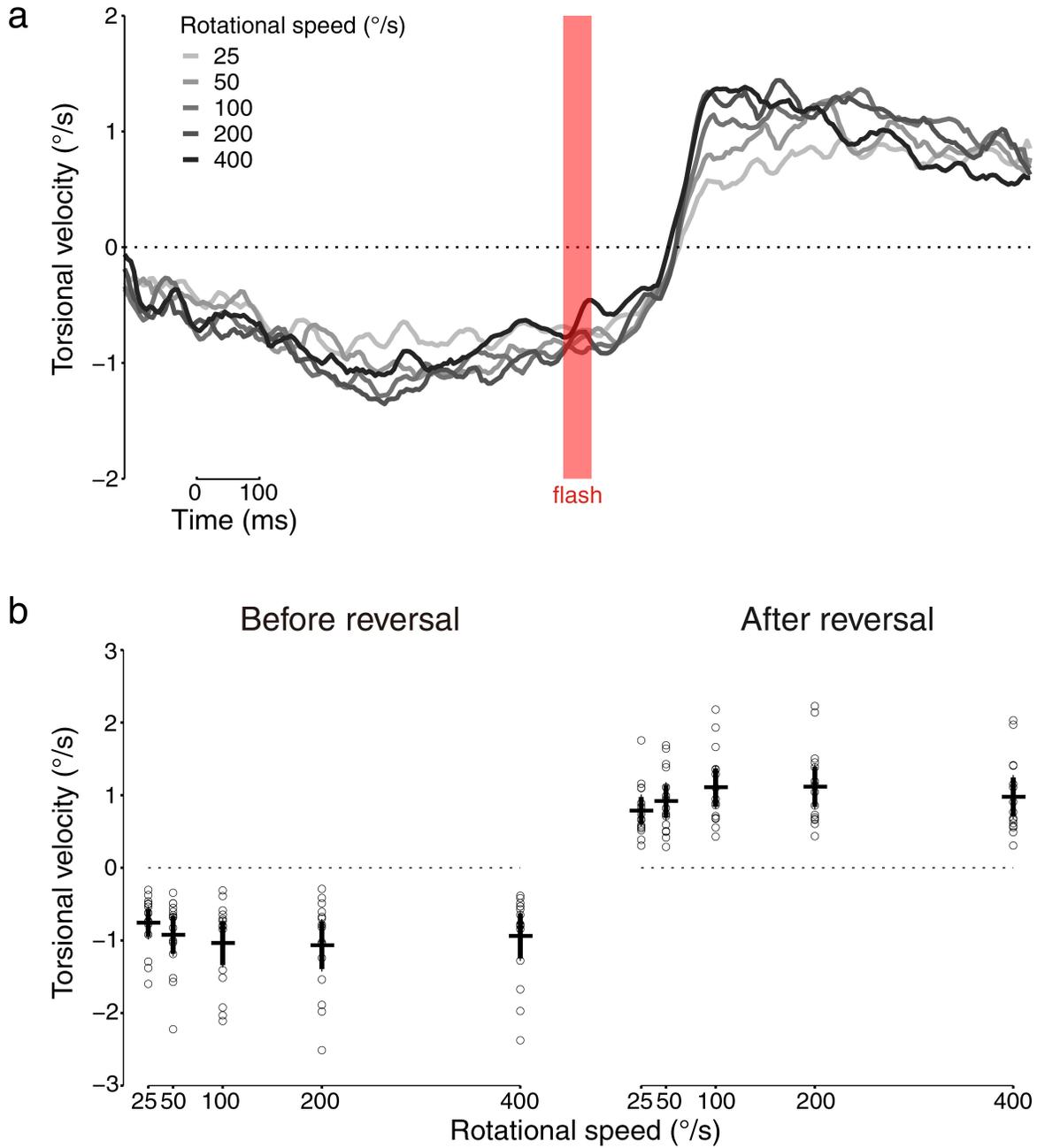
A single rotating grating induced the flash-grab effect and ocular torsion. The rotating stimulus in Experiment 1 successfully triggered the flash-grab effect: Observers perceived the flash to be tilted in the after-reversal motion direction, as indicated by all data points lying above zero shown in Figure 2.3. The magnitude of the illusory position shift increased with increasing rotational speed, confirmed by a main effect of *speed*,  $F(4, 56) = 53.26$ ,  $p < 0.001$ ,  $\eta_g^2 = 0.55$ . These results replicate previous reports of the flash-grab effect (Cavanagh and Anstis, 2013).



**Figure 2.3:** Illusory position shift across rotational speeds in Experiment 1 ( $n = 15$ ). Horizontal bars indicate the mean illusory position shift across observers (i.e., the perceived angle of the flash stimulus), and vertical bars indicate the 95% CI. The circles indicate the mean illusory position shift of individual observers. The dashed line indicates the veridical physical angle of the flash. CI, confidence interval.

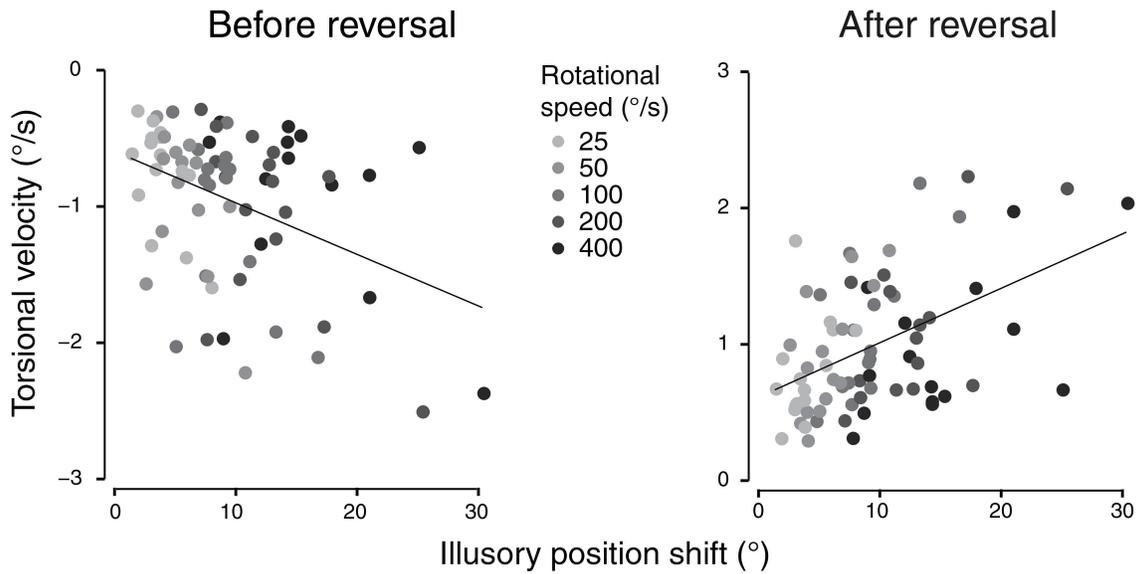
The single rotating grating induced reliable ocular torsion in the direction of visual stimulus rotation. Figure 2.4a shows mean velocity traces averaged across all observers separately for the five rotational speeds. Congruent with the observed effect of rotational stimulus speed on the strength of the perceptual illusion, rotational speed also affected how fast the eye rotated. Torsional velocity increased with increasing speed, saturating at a rotational speed of  $200^\circ/\text{s}$  (Fig. 2.4b). This observation is reflected in a significant main effect of *speed* before and after the reversal for torsional velocity: before reversal,  $F(4, 56) = 7.83$ ,  $p < 0.001$ ,  $\eta_g^2 = 0.04$ , and after reversal,  $F(4, 56) = 9.10$ ,  $p < 0.001$ ,  $\eta_g^2 = 0.06$ .

To examine the correlation between perception and torsion, we calculated Pearson's correlation coef-



**Figure 2.4:** (a) Torsional velocity traces averaged across all observers ( $n = 15$ ) in Experiment 1. Each colour indicates one rotational speed. Peak of torsional velocity scaled with rotational speeds. (b) Mean torsional velocity for each observer. Horizontal bars indicate the mean across observers, and vertical bars indicate the 95% CI. Circles indicate the mean of individual observers. CI, confidence interval.

ficients across observers between torsional velocity and illusory position shift, with speed as a covariate. Significant correlations were found for both time windows (before reversal:  $r = -0.49$ ,  $p < 0.001$ ; after reversal:  $r = 0.59$ ,  $p < 0.001$ ; see Fig. 2.5). Generally, observers with faster torsional eye rotations also perceived larger illusory position shifts. To confirm that the correlation was not caused by speed, we also calculated Pearson’s correlation coefficients using the collapsed data across speeds of each participant (one data point for each participant); significant correlations were still found for both time windows (before reversal:  $r = -0.56$ ,  $p = 0.03$ ; after reversal:  $r = 0.63$ ,  $p = 0.01$ ). In summary, results from Experiment 1 show that torsional velocity and perceptual illusion are correlated. We next investigated whether a causal relationship exists between them.



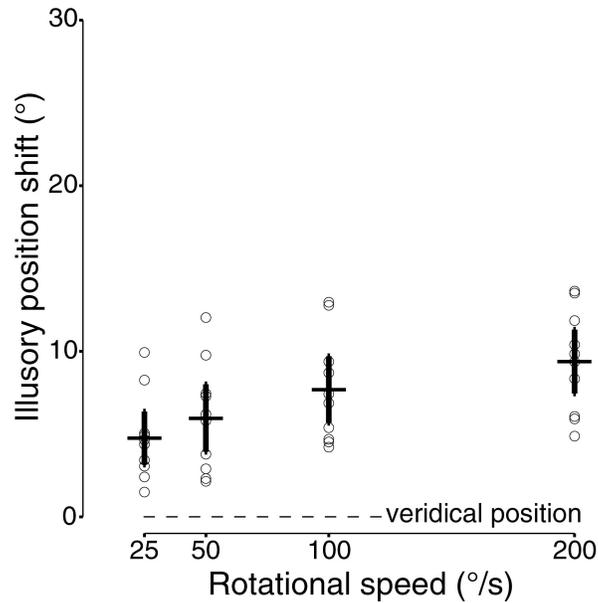
**Figure 2.5:** Correlation between torsional velocity and illusory position shift in Experiment 1 in both time windows. Each data point indicates the mean data of one speed of one observer. Black lines indicate the best linear fit.

## Experiment 2

Two rotating gratings induced the flash-grab effect in the absence of ocular torsion. The gratings shown in Experiment 2 produced a similar illusory position shift as in Experiment 1 (see Fig. 2.6). The magnitude of the illusory position shift increased with increasing rotational speed, confirmed by a main effect of *speed*,  $F(3, 27) = 58.10$ ,  $p < 0.001$ ,  $\eta_g^2 = 0.26$ .

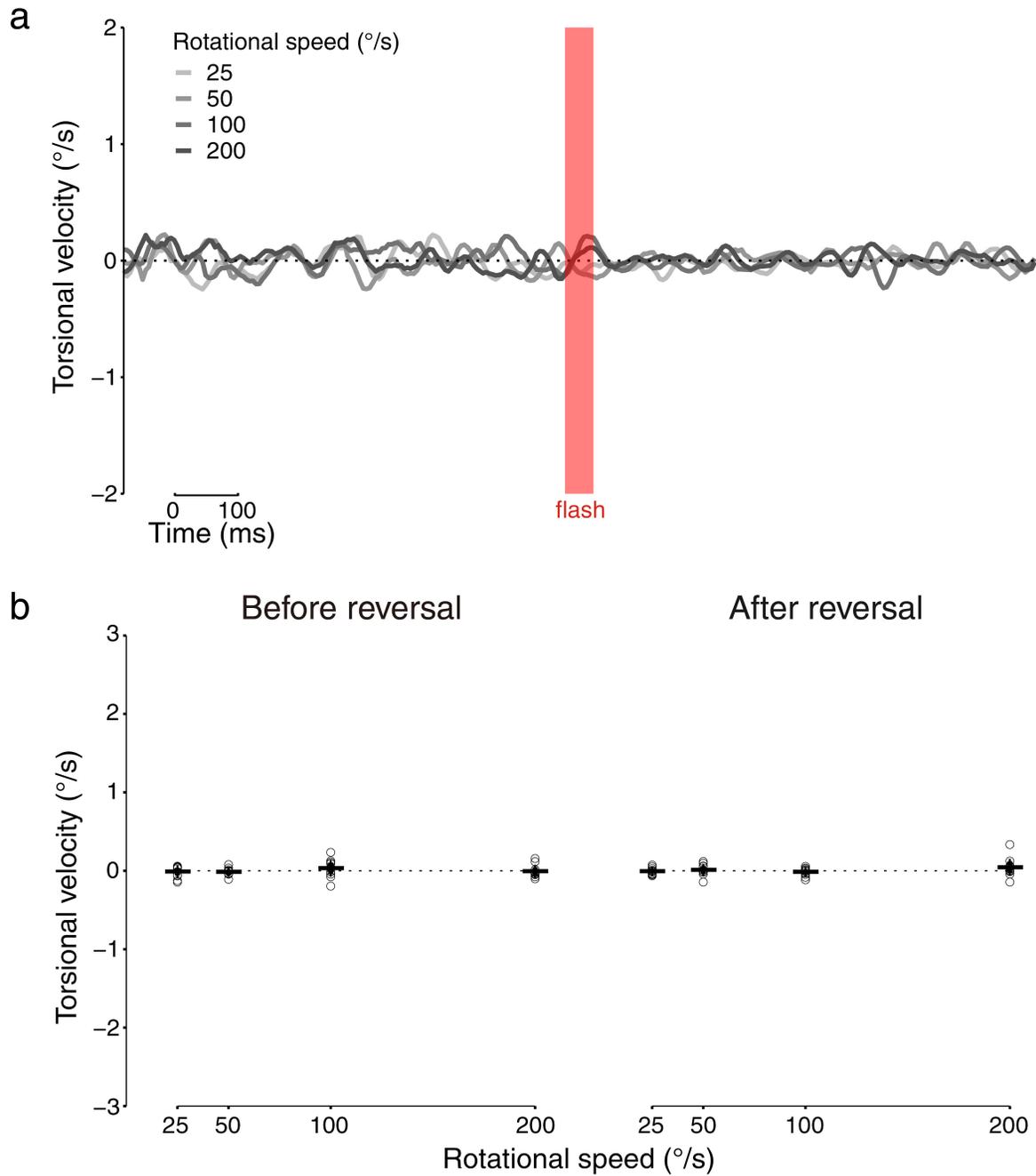
Eye velocity traces showed no trend for eye rotation in either of the gratings’ two possible rotational motion directions (Fig. 2.7a). This is expected because observers did not know which grating was going to be the target when viewing the rotation. We found no consistent torsional eye movements (see Fig. 2.7b) and no significant effects of rotational speed on torsional velocity: before reversal,  $F(3, 27) = 0.57$ ,  $p = 0.64$ ,  $\eta_g^2 = 0.05$ , and after reversal,  $F(3, 27) = 1.14$ ,  $p = 0.35$ ,  $\eta_g^2 = 0.08$ .

To confirm that the selection of single eye data in each trial did not eliminate any systematic torsional

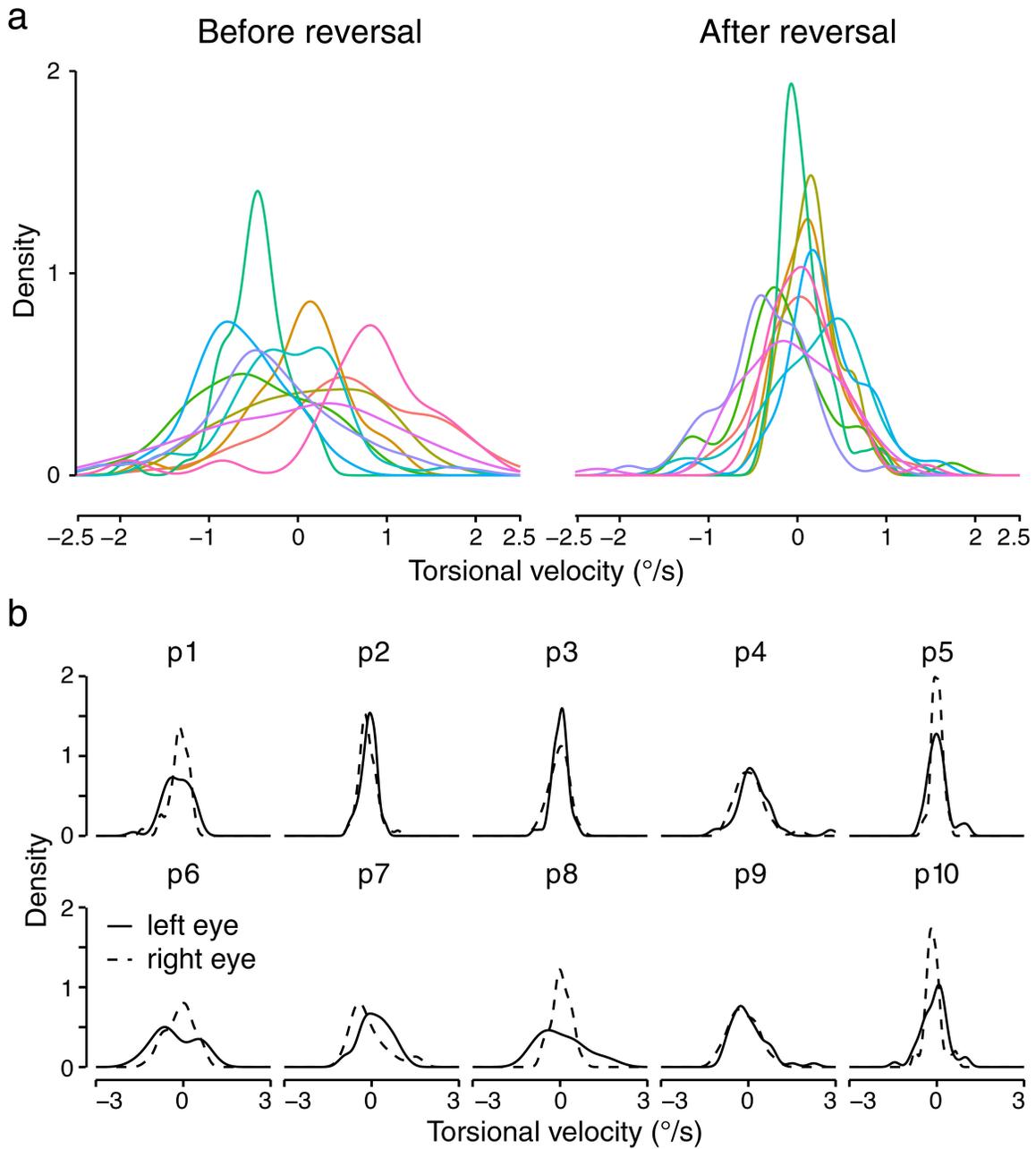


**Figure 2.6:** Illusory position shift across rotational speeds in Experiment 2 ( $n = 10$ ). Horizontal bars indicate the mean across observers, and vertical bars indicate the 95% CI. Circles indicate the mean of individual observers. CI, confidence interval.

eye movements, we plotted the density of each observer's torsional velocity (see Fig. 2.8a). This is to examine the possibility that the eyes randomly followed one rotating grating in each trial (i.e., selected one of the two gratings as a target). If the eyes rotated to different directions in each trial, we should expect two peaks in each observer's density plot. However, none of the observers showed two clearly distinguishable peaks, indicating little eye rotations following any particular rotational motion direction. To further confirm that no cyclovergence was induced, we also examined torsional velocity in each eye separately for each participant. Trials were collapsed so that the initial rotational direction of the left stimulus was always CW: If cyclovergence occurred, torsional velocity of the left eye should peak at a positive value before reversal and at a negative value after reversal, and vice versa for torsional velocity of the right eye. However, the torsional velocity of both eyes had similar peaks around zero for all participants in all time windows and speeds (Fig. 2.8b). These results indicate that two oppositely rotating gratings did not induce reliable torsional eye movements. Congruently, we found no correlation between torsional velocity and illusory position shift across observers (before reversal:  $r = 0.09$ ,  $p = 0.59$ ; after reversal:  $r = 0.07$ ,  $p = 0.68$ ). Taken together, the persistence of the perceptual illusion and the elimination of consistent torsional eye movements in Experiment 2 indicate that there is no causal relationship between torsion and motion perception in the illusion under study.



**Figure 2.7:** (a) Torsional velocity traces averaged across all observers ( $n = 10$ ) in Experiment 2. Each colour indicates one rotational speed. (b) Mean torsional velocity for each observer. Horizontal bars indicate the mean across observers, and vertical bars indicate the 95% CI. Circles indicate the mean of individual observers. CI, confidence interval.



**Figure 2.8:** Density of torsional velocity in response to a visual rotational speed of  $200^{\circ}/s$  in Experiment 2. (a) Individual torsional velocity of both eyes in each time window. Each line denotes one participant ( $n = 10$ ). (b) Torsional velocity of each eye in each participant (p1–p10) in the after-reversal time window. Results from other speeds or time windows are similar.

#### 2.1.4 Discussion

Torsional eye rotations are ubiquitous during visual perceptual tasks because they accompany almost every gaze shift. Yet most experimental studies on perception ignore torsion. Here we used a well-established

perceptual illusion, the flash-grab effect, as a test bed for the idea that torsional eye movements interact with visual motion perception. We report two key findings. First, a centrally presented large-field rotational motion stimulus triggered reliable illusory position shifts and torsional eye movements in the direction of the illusion. Importantly, the magnitude of illusion and torsion were correlated, and both responses scaled similarly with rotational stimulus speed. Second, the perceptual illusion persisted in the absence of systematic ocular torsion. Even though torsion does not cause perceptual illusion, our findings indicate cross-talk between the perceptual and torsional eye movement system. These results are congruent with studies that have observed similar relationships between illusory motion perception and saccades (van Heusden et al., 2018) or pursuit (Braun et al., 2006; Watamaniuk and Heinen, 2007).

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

In a broader context, our results reveal a close link between visually-induced torsion and motion perception. Previous studies have shown a link between oblique eye position-induced torsion or self-motion-induced torsion and perception: The perceived orientation of a line was biased in the direction opposite to torsional eye position (Haustein and Mittelstaedt, 1990; Murdison et al., 2019; Nakayama and Balliet, 1977; Wade et al., 1991). The link between torsion and orientation perception indicates that torsional eye position itself biases perception. In the current study, it remains possible that torsional eye rotation enhances the illusory position shift by causing a bias in orientation perception of the flash. However, testing torsion's contribution to the illusion would require direct manipulation of torsional eye movements, for example, by temporally paralyzing extraocular muscles (i.e., the superior obliques) to prevent rotations while observers view and evaluate visual motion. It is also important to note that torsional eye movements are very small rotations of the eye; thus, any changes in torsion or its contribution to perception could easily be masked by noise. In seven participants, we attempted to mechanically manipulate torsion by asking them to view the illusion during a 50° head tilt, known to induce ocular counter-roll to the opposite direction of the head tilt (Collewijn et al., 1985; Hamasaki et al., 2005). We expected that this manipulation would yield a stable counter-roll position and limit any further effects of visual rotational motion on torsion. However, the induction of head tilt did not result in consistent reduction of torsion across participants, probably because convergence

when viewing a close target reduces ocular counter-roll (Ooi et al., 2004). Instead, head tilt caused larger perceptual noise, thus not allowing us to investigate the limiting effects of abolishing torsion on perception.

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

### **Neural correlates of a torsion-perception link**

Because torsion and the illusion are induced by rotational motion and are correlated, one possibility is that both systems are triggered by similar input signals. Neurons in the dorsal division of the medial superior temporal area (MSTd) have large receptive fields and are sensitive to rotational motion (Graziano et al., 1994; Mineault et al., 2012; Tanaka et al., 1989). Neurons in this area are also tuned to vestibular rotation signals (Takahashi et al., 2007). There is no direct evidence linking activity in the MSTd to the generation of ocular torsion. However, neurons in cortical motion-processing areas such as the MSTd project to pontine nuclei in the brainstem and then to the cerebellar cortex for the generation of smooth pursuit eye movements. It is therefore possible that similar pathways also connect MSTd with brainstem areas responsible for the generation of torsion (i.e., the rostral interstitial nucleus of the medial longitudinal fasciculus for torsional quick phases, and the interstitial nucleus of Cajal for torsional slow phases; for reviews, see Klier et al. 2013; Leigh and Zee 2015). It is unclear whether motion-processing areas such as the MST are directly responsible for the generation of motion-induced illusions, such as the flash-grab effect. Human electroencephalography (EEG) and functional neuroimaging studies suggest that these illusions might be related to activity in the earliest visual cortical areas, predominantly areas V1– V3 (Hogendoorn et al., 2015; Kohler et al., 2017), but higher-level motion-processing areas likely play a role as well. A study using a dichoptic display suggests that the flash-grab illusion might be the manifestation of a hierarchical predictive coding framework, which extends from monocular processing stages (from retina to lateral geniculate nucleus) to binocular processing stages beyond V1 (van Heusden et al., 2019). It is possible that motion-processing signals from the MST were obtained by both torsional and perceptual systems, but whereas the perceptual system can use local motion information with opposite motion directions, the torsional system may rely on global motion, yielding the dissociation in responses in Experiment 2.

In addition to coding retinal motion, the MST also receives extraretinal signals related to eye-in-head movement and directly projects to the frontal pursuit area (FEFsem; Churchland and Lisberger 2005). These areas might thus play a role in integrating visual and non-visual efference copy signals (Bakst et al., 2017; Nuding et al., 2008; Ono and Mustari, 2012). Stronger torsional eye movements such as those observed in Experiment 1 might trigger a signal boost in areas MST and FEFsem via feedback connections, contributing to the illusion.

In conclusion, similar motion input for torsion and perception and feedback signals could be responsible

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

## **2.2 On the relation between anticipatory ocular torsion and anticipatory smooth pursuit**

In the previous study, we found a correlation between perception and visually-induced torsion, suggesting potentially shared motion processing of sensory signals. To further examine to what extent torsion is under cognitive control, in this study<sup>2</sup> we test whether and how anticipatory torsion can be induced. Specifically, as it has been shown that anticipatory pursuit can be elicited by various types of cues (Kowler, 1989; Santos and Kowler, 2017), we examine and compare anticipatory torsion and anticipatory pursuit under the same conditions.

### **2.2.1 Introduction**

Real-world movements, ranging from catching prey to hitting a ball, require rapid prediction of an object's trajectory from a brief glance at its motion. It is well-established that smooth pursuit eye movements can be initiated several hundred milliseconds before the onset of object motion, if the direction of the moving target is known in advance (Badler and Heinen, 2006; Barnes and Collins, 2008; Blohm et al., 2003a,b; Boman and Hotson, 1988; de Hemptinne et al., 2006; Dodge et al., 1930; Kowler, 1989, 2011; Kowler et al., 2014; Westheimer, 1954). These eye movements reflect processes of anticipation of a future motion path, and compensate for sensorimotor delays in situations that require fast decisions or actions (Borghuis and Leonardo, 2015; Brenner and Smeets, 2000; Nijhawan, 1994; Wolpert et al., 1995).

Anticipatory smooth pursuit eye movements generally occur when target motion is predictable. Such predictions can be based on strong expectations of an upcoming motion direction (Fiehler et al., 2019). At the lowest processing level, these could be induced by repeatedly showing the same kind of stimulus, such as when trials with rightward and leftward target motion are grouped into separate blocks. Stimulus repetition primarily leads to habitual or priming responses through relatively low-level learning processes (Kowler, 1989) in combination with expectation of the upcoming motion based on trial history. Another way of inducing expectation is by presenting targets in a particular configuration that acts as a visual cue, such as when a fixation spot on the left side of the screen will always be followed by rightward target motion. Finally, higher-level symbolic cues have been particularly powerful in eliciting anticipatory pursuit, for example, when a barrier on the left indicates rightward target motion (Kowler, 1989; Kowler et al., 2014).

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<sup>2</sup>A version of this study has been published as Rothwell, A. C., Wu, X., Edinger, J., and Spring, M. (2020). On the relation between anticipatory ocular torsion and anticipatory smooth pursuit. *Journal of vision*, 20(2):1–12. Contents are almost identical except for: 1. Editorial changes (e.g., changing "visually guided torsion" to "visually-guided torsion") to keep a consistent formatting throughout the dissertation; 2. Clarification of task design in experiments 1-3 in Methods ("Procedure, design, and task"), and of the variables and factors in rmANOVA ("Statistical analysis").

Such symbolic cues can supersede effects of stimulus repetition or simple visual cues (Kowler, 1989; Kowler et al., 2014; Ladda et al., 2007). Different cue types interact differently with the probabilistic information they convey about target motion (Santos and Kowler, 2017). When target motion is entirely unpredictable, anticipatory pursuit can still be based on an estimate of target motion probability, derived from memory and past experience (Barnes and Collins, 2008; de Hemptinne et al., 2007; Heinen et al., 2005; Santos and Kowler, 2017). In summary, anticipatory pursuit eye movements can be driven by a combination of visual and cognitive factors that involve learning of perceptual configurations or simple cues and memory of past history.

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

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

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

## **2.2.2 Methods**

### **Observers**

We recruited 18 observers (mean age = 25.5,  $SD = 4.9$  years, seven women) with normal and uncorrected

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

### **Visual stimuli and setup**

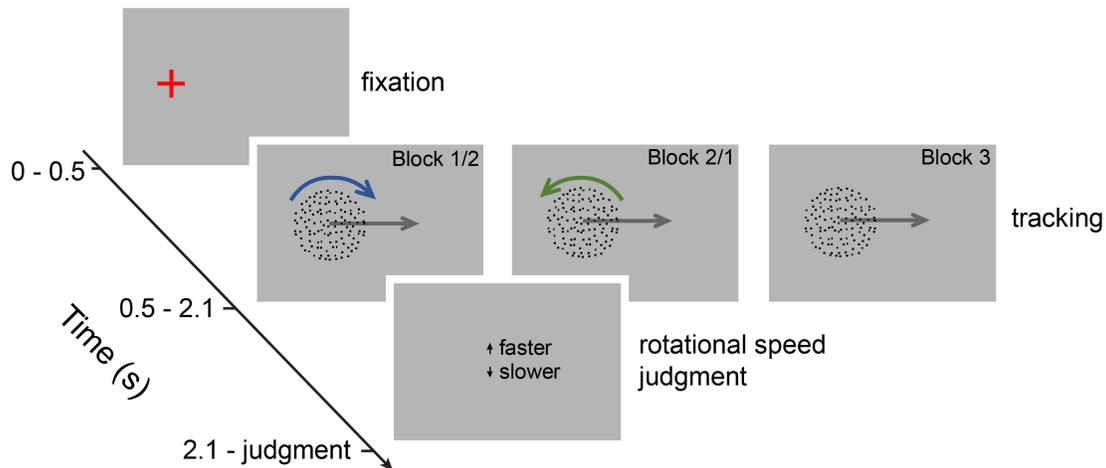
Stimuli were random dot patterns (RDP) presented within a disk of  $8^\circ$  diameter on a uniform white background ( $55 \text{ cd/m}^2$ ). The RDP consisted of 400 uniformly distributed black dots ( $0.05 \text{ cd/m}^2$ ) that were stationary within the disk, each with a diameter of  $0.15^\circ$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

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

### **Procedure, design, and task**

Each block started with a five-point eye-tracker calibration on targets spaced  $10^\circ$  apart on a  $20^\circ \times 20^\circ$  grid. In Experiments 1 and 2, trials began with fixation on a red cross (size  $1^\circ$ ) at a peripheral location  $8^\circ$  to the left or right of the screen centre presented for 450 ms (Fig. 2.9). After a 50-ms interval, the RDP stimulus appeared at the location of the fixation cross and moved across the screen for 1600 ms. The stimulus had the appearance of a rolling ball when rightward translational stimulus motion was combined with CW stimulus rotation (as shown in Fig. 2.9, left), or when leftward translational motion was combined with CCW rotation; we refer to this pattern as “natural” and to the opposite pattern as “unnatural” (shown in Fig. 2.9, middle). A previous study showed that torsional velocity gain is higher when tracking the natural pattern than when tracking the unnatural pattern (Edinger et al., 2017). Therefore, we included both patterns in Experiments 1 and 2 to examine whether anticipatory torsion might differ between the two patterns.

In Experiment 1, horizontal target motion to the right or left was presented in separate blocks of trials. The purpose of this repetition of motion direction within each block was to trigger anticipatory pursuit. Within each series of “left” or “right” blocks, rotational motion direction—either natural or unnatural—was also presented in separate blocks of trials. For example, in a “right natural” block, rightward motion direction was paired with CW rotation; in a “right unnatural” block, rightward motion direction was paired with CCW

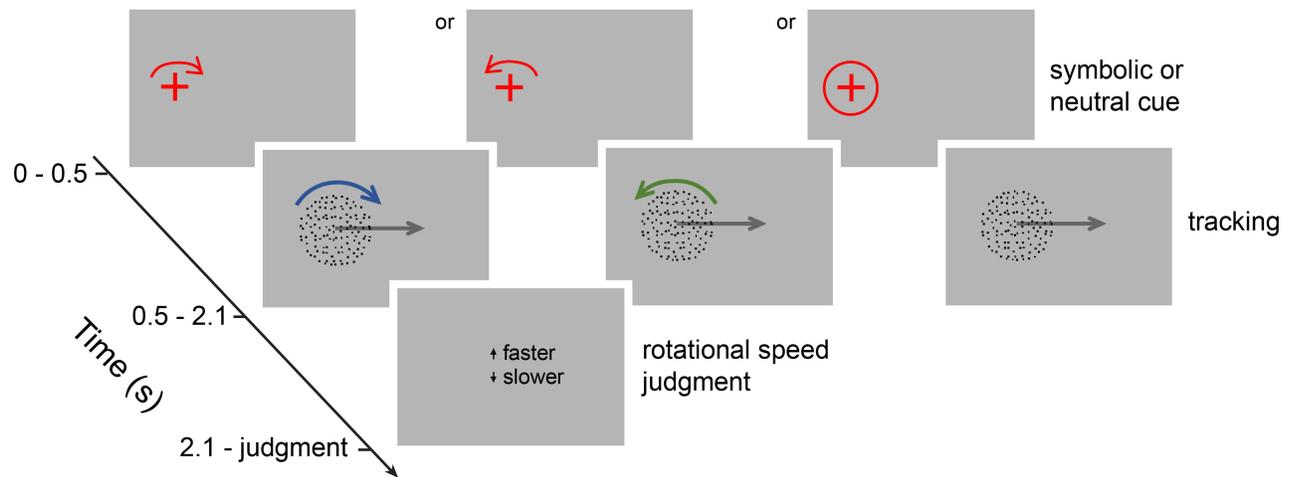


**Figure 2.9:** Design and trial timeline in Experiment 1. Each trial began with fixation on a peripheral fixation cross, shown for 450 ms, followed by an interstimulus interval of 50 ms. The rotating target was shown for 1600 ms, followed by a screen prompt to give a perceptual judgment by pressing the up (faster) or down (slower) key on a computer keyboard.

rotation. The purpose of this was to elicit anticipatory torsion. Order of blocks with stimulus rotation (left, right, natural, or unnatural first) was randomized. In each trial, observers judged whether the rotational speed of the stimulus was faster or slower than the average across all previous trials by pressing an assigned key on a computer keyboard. The purpose of this task was primarily to direct observers' attention to the rotation of the stimulus. The next trial started immediately after the observer indicated their response on the computer keyboard. We also included a baseline condition with rightward or leftward target motion and no rotation (Fig. 2.9, right); these blocks were always presented last. In total, this experiment consisted of six blocks of 200 trials each, run in two separate sessions of no more than 60 minutes each.

In Experiment 2, trials with leftward and rightward translational direction and with natural, unnatural, or no rotation were presented in randomly interleaved order within the same block of trials. Upcoming horizontal direction was 100% predictable based on the location of the fixation cross, that is, fixation on the left was always followed by motion to the right, and vice versa. Upcoming target rotation was indicated by a cue presented above or below the fixation cross for 450 ms. The cue was either an arrow indicating CW or CCW rotational direction, or a circle around fixation indicating no rotation in the upcoming trial (Fig. 2.10). As in Experiment 1, the location of the fixation cross and cue indicated upcoming horizontal target motion reliably (100% validity). This experiment included three blocks of 200 trials each, run in one single 60-minute session.

In Experiment 3, to further examine whether different types of symbolic cues affect anticipatory torsion differently, we designed an experimental condition with higher-level symbolic cues similar to the barrier cue developed by Kowler (1989). In previous studies, the pursuit target moves down a tube which splits into two directions. The barrier cue blocks one of the tubes, leaving only one possible direction for the target to go to

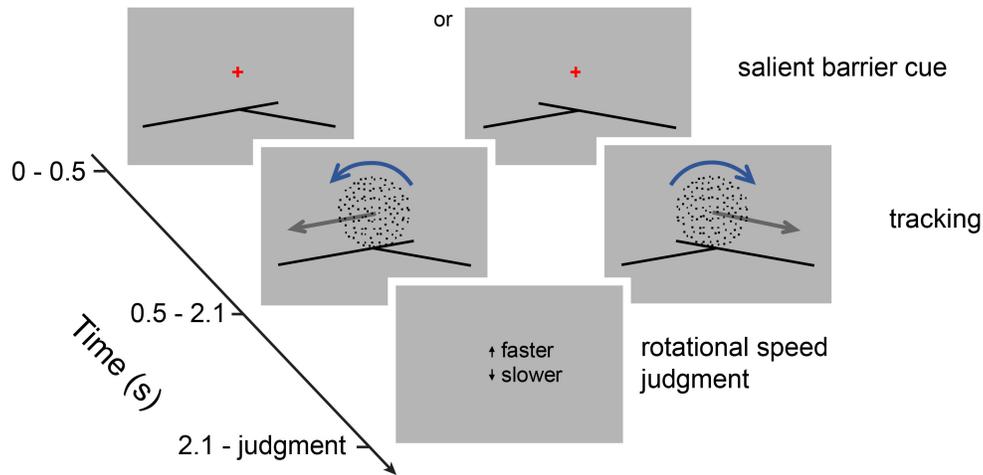


**Figure 2.10:** Design and trial timeline in Experiment 2. A symbolic, visual cue was shown during the fixation period, indicating with 100% validity the target’s rotation direction in the upcoming trial. Target presentation duration and perceptual task were identical to Experiment 1.

(Kowler et al., 2014; Santos and Kowler, 2017). This barrier cue has a stronger effect on anticipatory pursuit than trial repetition or simple symbolic cues, such as arrows (Kowler et al., 2014; Santos and Kowler, 2017). Instead of tubes for the target to move down, we presented slopes along which the RDP might roll down. The RDP moved along one of two diagonal line segments that each had a  $10^\circ$  slope (Fig. 2.11). The RDP still translated at the same speed of  $10^\circ/s$ , thus the horizontal speed was slightly lower ( $9.8^\circ/s$ ) than in the other experiments. The fixation cross was centred at the RDP’s start position. In the first block of trials, the RDP moved leftward or rightward with no rotation; in the second block, translational motion was combined with natural stimulus rotation. We only presented natural rotation in this experiment so that the direction of the slope corresponded to the rotational direction of the RDP intuitively. In both blocks, leftward and rightward motion directions were randomly interleaved. Upcoming target direction was indicated with a 100%-valid barrier cue ( $4^\circ$  long extension of the slope above the crossing point) presented from the onset of fixation in all blocks. An extension of the line segment tilted from the upper left to lower right part of the screen, for example, indicated upcoming motion to the right. Each block contained 200 trials, and the experiment was run in one single 30-minute session.

### Eye movement recordings and analysis

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



**Figure 2.11:** Design and trial timeline in Experiment 3. Following central fixation, the RDP translated down the slope in the motion direction opposite to the indicated barrier. In block 1, the RDP did not rotate, in block 2, a natural rotation direction was always shown. The barrier cue indicated with 100% validity the upcoming target’s translational direction in both blocks, and the target’s rotational direction in block 2. Target presentation duration and perceptual task were identical to Experiment 1.

Three-dimensional eye-in-head position data were processed offline for each eye separately using the Chronos Iris software (Version 1.5) to derive horizontal, vertical, and torsional eye position data from video recordings. The principle of deriving torsional eye position data relies on interframe changes in the iris crypt landmark with each eye rotation. Following standard practice, ocular torsion was obtained from cross-correlation between iris segments across images. Four segments were fitted to each eye’s iris and angular eye position was calculated as a weighted average from all segments with a cross correlation factor of  $> 0.7$ . By convention, leftward, downward, and extorsion (i.e., the top of the eye moving away from the nose) of the right eye and intorsion (the top of the eye moving toward the nose) of the left eye are positive.

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

stimulus onset to 50 ms after stimulus onset, yielding the magnitude of anticipatory torsion and pursuit, respectively.

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

### **Statistical analysis**

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

### **2.2.3 Results**

#### **Direction repetition and direction cues reliably trigger anticipatory horizontal pursuit**

The stimulus configuration in our paradigm—fixation position to the left or right of screen centre combined with centripetal target motion, or the presence of the barrier cue—made the target's horizontal motion direction predictable. As a result, observers reliably initiated anticipatory horizontal pursuit in the direction of the upcoming target, starting on average 200 ms before motion onset in both experiments. These findings are demonstrated in mean horizontal eye velocity traces for all three experiments (Fig. 2.12). Interestingly,

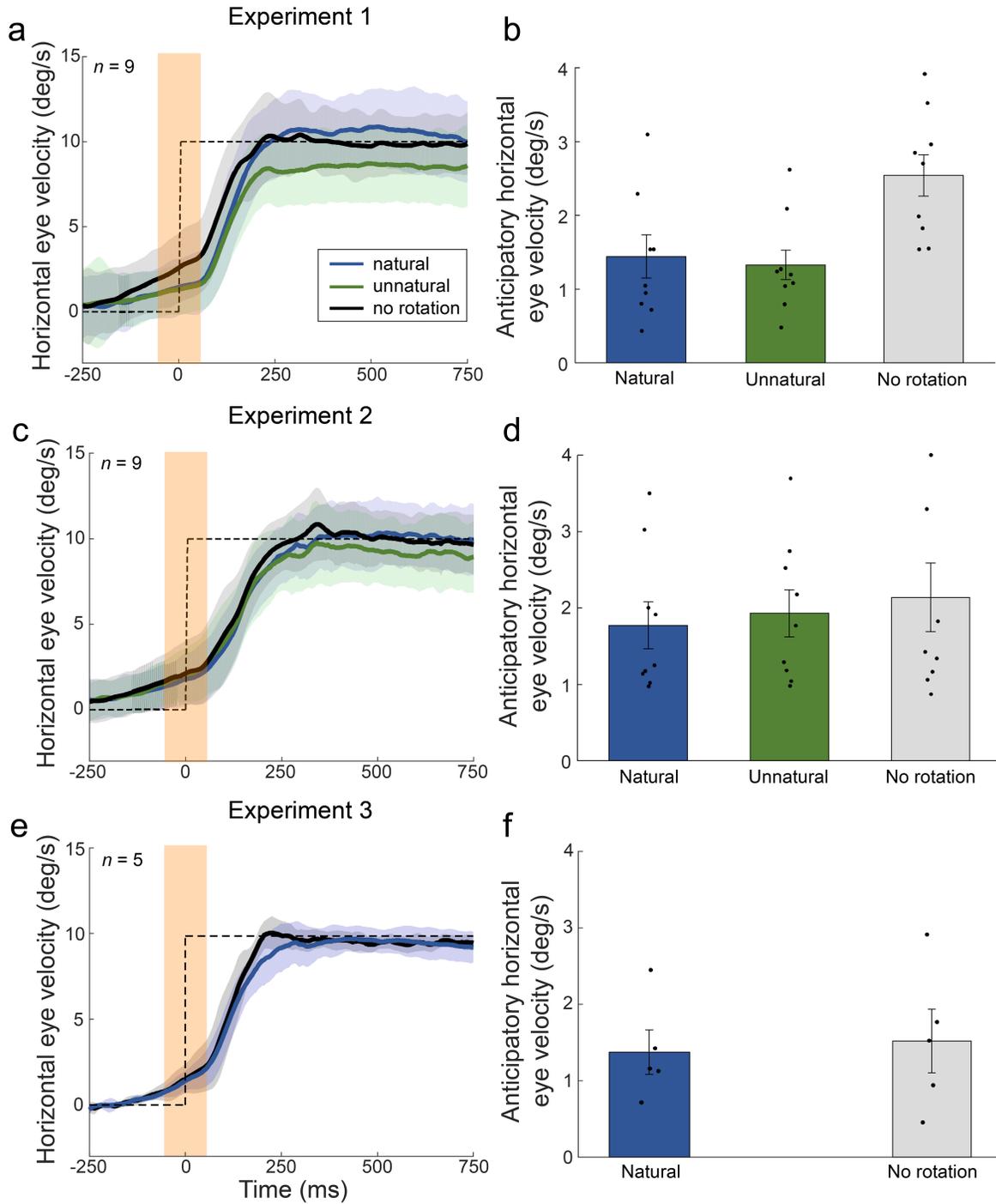
in Experiment 1, anticipatory horizontal pursuit velocity differed depending on whether the stimulus rotated or not (Fig. 2.12b). This observation was confirmed by a main effect of *rotation* on anticipatory pursuit velocity,  $F(2, 16) = 25.26, p < 0.001, \eta^2 = 0.76$ . Anticipatory pursuit velocity was significantly reduced in comparison to the no-rotation baseline when the stimulus rotated naturally [ $t(8) = 7.27, p = 0.02$ ] and unnaturally [ $t(8) = 6.83, p = 0.01$ ]. Even though the magnitude of anticipatory pursuit velocity was comparable across experiments [Experiment 1:  $M = 1.74^\circ/s, std = 0.72$ ; Experiment 2:  $M = 1.95^\circ/2, std = 1.04$ ; Experiment 3:  $M = 1.45^\circ/s, std = 0.78$ ;  $F(2, 20) = 0.53, p = 0.60, \eta^2 = 0.05$ ], it did not depend on stimulus rotation in Experiments 2 and 3. These observations are confirmed by a lack of significant main effect of *rotation* for Experiment 2 [natural vs. unnatural vs. no rotation;  $F(2, 16) = 2.03, p = 0.19, \eta^2 = 0.20$ ], and Experiment 3 [natural vs. no rotation;  $F(1, 4) = 0.70, p = 0.45, \eta^2 = 0.15$ ].

### **Only stimulus repetition, not symbolic cues, elicit anticipatory torsion**

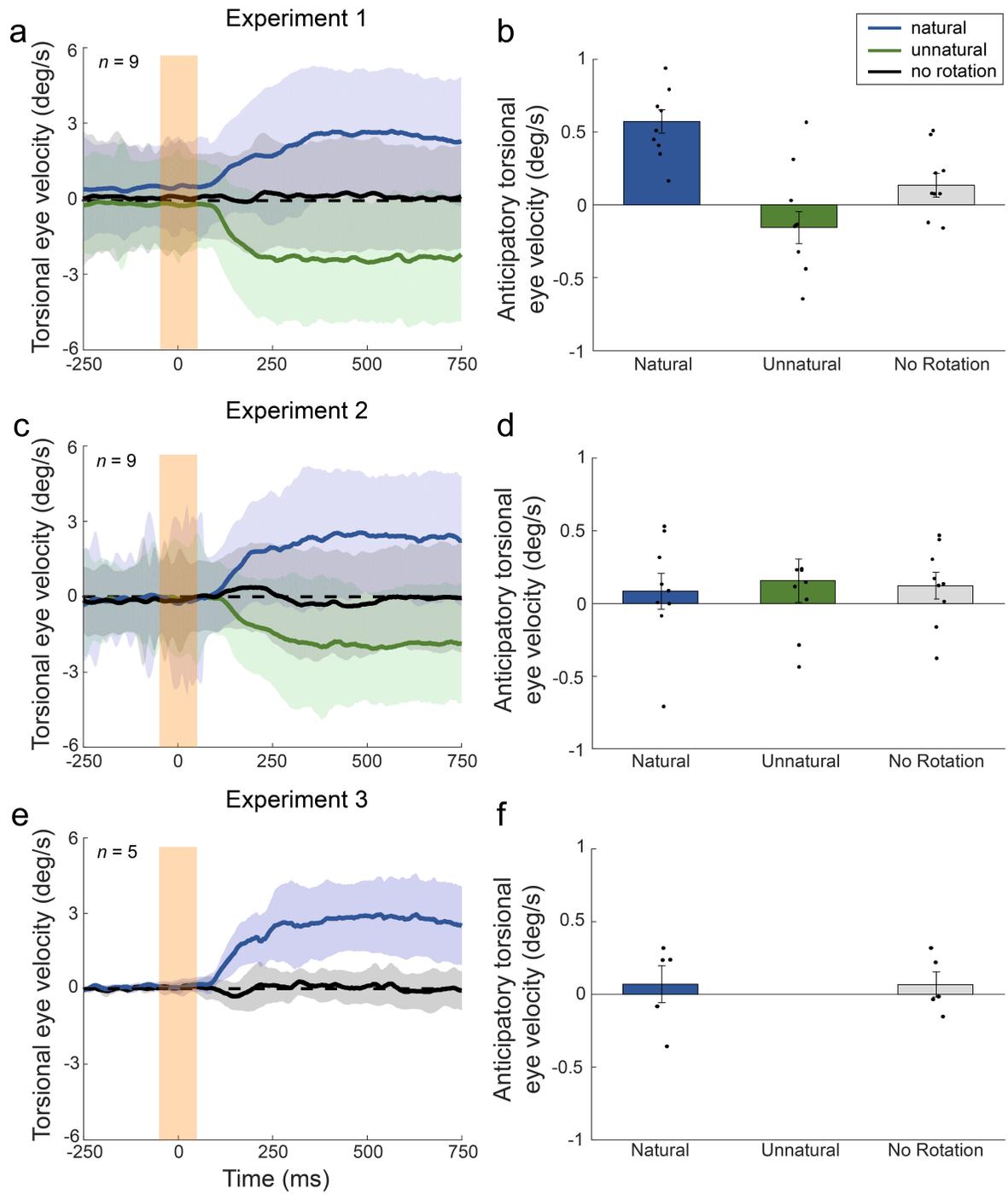
Importantly, we found that observers anticipated the target’s rotational direction. The eyes rotated about the visual axis either CW in response to “natural” or CCW in response to “unnatural” rotation prior to target onset. Figure 2.13a shows mean torsional velocity traces for Experiment 1, revealing a separation of responses to natural versus unnatural rotation several hundred milliseconds prior to target motion onset. These observations are reflected in comparisons of mean torsional eye velocity during the same interval as anticipatory smooth pursuit, from 50 ms before to 50 ms after target onset, in Experiment 1 (Fig. 2.13b). Rotational direction had a significant main effect on mean anticipatory torsional velocity,  $F(2, 16) = 14.6, p < 0.005, \eta^2 = 0.65$ , mostly driven by the difference between natural rotation and no rotation [ $t(8) = 3.94, p < 0.004$ ]. The difference between unnatural rotation and the no-rotation baseline was non-significant when corrected for multiple comparisons [ $t(8) = 2.21, p = 0.15$ ] because mean anticipatory torsion was overall weaker in response to unnatural rotation. These findings indicate that anticipation of rotational motion direction, triggered by stimulus repetition, can modulate ocular torsion, especially in response to a naturally rotating stimulus that causes stronger torsion overall (Fig. 2.14a). By contrast, cognitive expectation triggered by a symbolic cue did not modulate ocular torsion, regardless of whether this cue was paired with a particular stimulus configuration (location of the fixation cross as a stationary visual cue, Experiment 2) or whether it was used in isolation (Experiment 3). Results from these two experiments reveal no anticipatory torsion (Fig. 2.13c, e) and no significant main effect of rotational direction (natural, unnatural vs. no rotation in Experiment 2, or natural vs. no rotation in Experiment 3) on torsional velocity (Fig. 2.13 d, f; both  $F < 1$ ). Although the magnitude of anticipatory torsion in Experiment 1 was correlated with the magnitude of visually-guided torsion, there was no such relationship between anticipatory and visually-guided torsion in Experiments 2 and 3 (Fig. 2.14b).

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

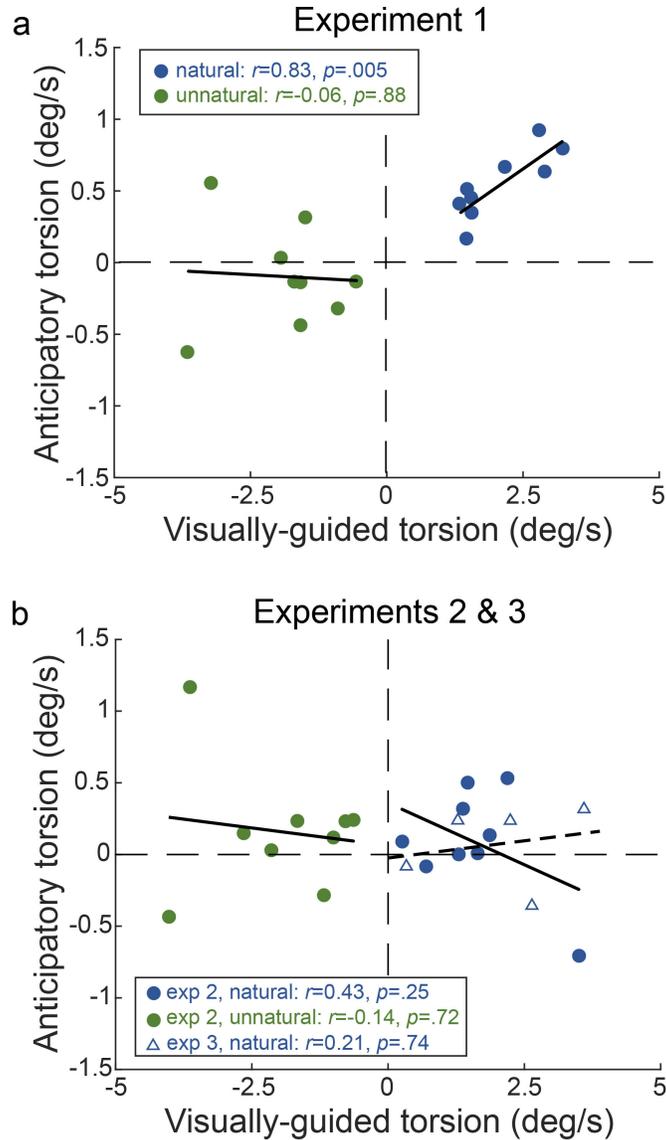
The results described so far are based on averages across all trials in a given block. We next investigated how anticipatory pursuit and anticipatory torsion built up over the course of a block of trials, and compared



**Figure 2.12:** Horizontal smooth pursuit eye movements in response to anticipated and visual target motion. (a, c, e) Mean horizontal eye velocity traces in Experiments 1 ( $n = 9$ ), 2 ( $n = 9$ ), and 3 ( $n = 5$ ). Shaded areas denote between-subject standard deviations. (b, d, f) Mean anticipatory horizontal eye velocity in the interval from 50 ms before to 50 ms after target motion onset; each data point indicates the mean for one observer in Experiments 1, 2, and 3. Error bars denote standard error of the mean.



**Figure 2.13:** Torsional eye movements in response to anticipated and visual target rotation. (a, c, e) Mean torsional eye velocity traces in Experiments 1 ( $n = 9$ ), 2 ( $n = 9$ ), and 3 ( $n = 5$ ). Shaded areas denote between-subject standard deviations. (b, d, f) Average anticipatory torsional eye velocity in Experiments 1, 2, and 3. Each data point indicates the mean for one observer. Error bars denote standard error of the mean.



**Figure 2.14:** Comparison of the magnitude of visually-guided torsion and anticipatory torsion in (a) Experiment 1 and (b) Experiments 2 and 3. Black lines indicate best-fit linear regressions. Each data point represents the mean for one observer.

the temporal development for anticipatory pursuit and torsion. Figure 2.15 shows anticipatory eye velocity accumulated over time, that is, eye velocity at trial = 1 is the anticipatory eye velocity in trial 1 for all observers; eye velocity at trial = 10 is the eye velocity averaged across trials 1-10 for all observers. In Experiment 1, anticipatory pursuit responses built up quickly within the first five trials (Fig. 2.15a). Accumulation profiles were similar in all conditions, despite differences in anticipatory pursuit magnitude (see Fig. 2.15c, e). In Experiment 2, anticipatory pursuit built up faster in trials in which the stimulus rotated as compared with no-rotation trials (Fig. 2.15c), possibly indicating the cost of decoding the neutral cue in

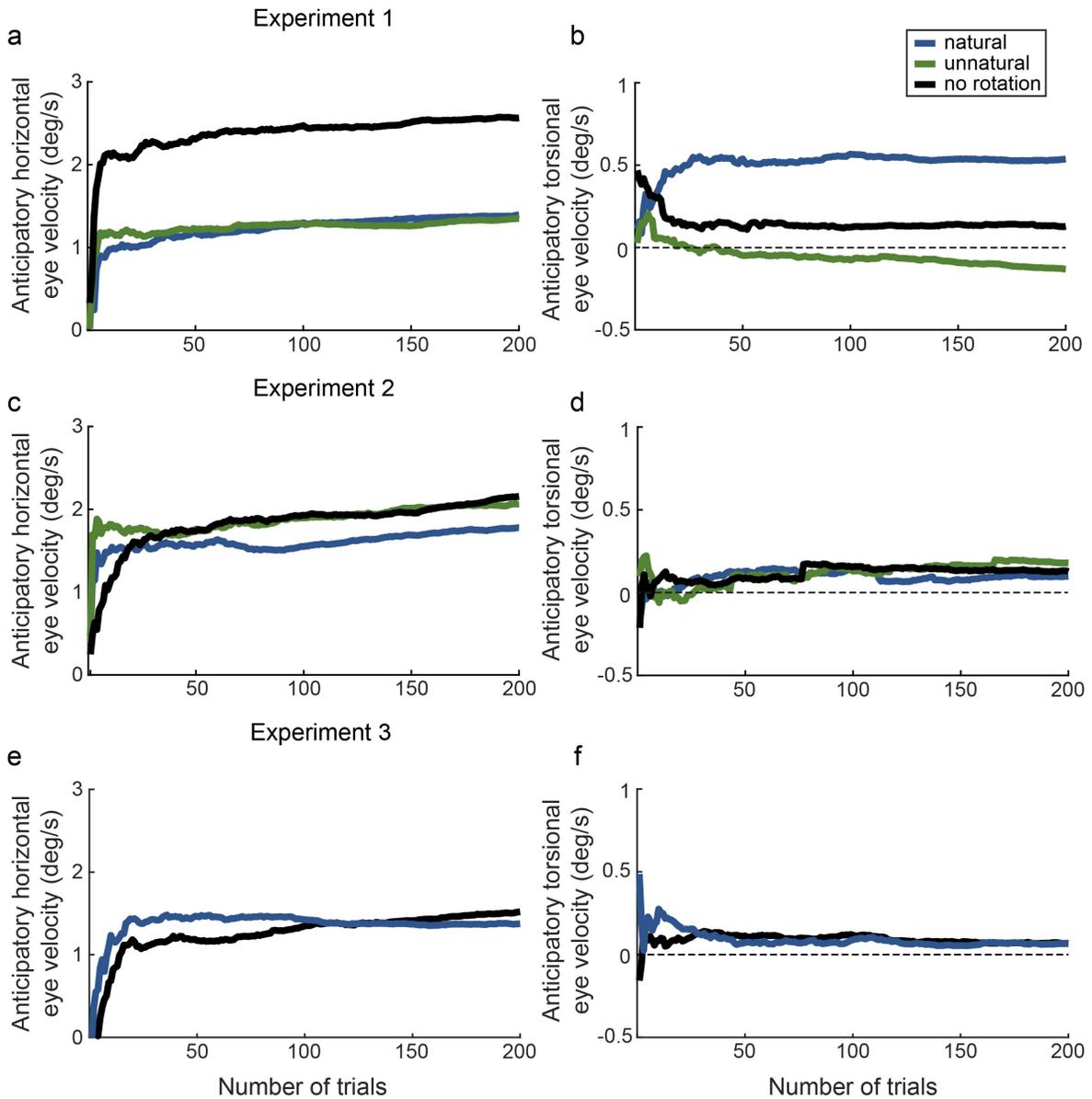
that condition. In Experiment 3, anticipatory pursuit built up more slowly than in Experiments 1 and 2 (Fig. 2.15e), possibly because the translational direction in Experiment 3 was only indicated by the barrier cue, not by an additional stationary cue (location of fixation spot).

The temporal development of anticipatory torsion in Experiment 1 was slower than for anticipatory pursuit; anticipatory torsion took approximately 20 trials to reach its maximum (Fig. 2.15b). There was no notable change in the anticipatory torsional velocity response in Experiment 2 (Fig. 2.15d) or in Experiment 3 (Fig. 2.15f). The comparison between anticipatory pursuit and torsion in Experiment 1 indicates that low-level visual signals derived from stimulus repetition or priming drives both responses, but at a different temporal rate.

To isolate the effect of longer-term cognitive expectation, we randomized the order of motion directions in Experiments 2 and 3. However, it is still possible that short-term priming effects might have occurred due to recent trial history (Heinen et al., 2005; Kowler, 1989). To investigate the effect that the preceding trials might have had on anticipatory pursuit and torsion in a given trial, we conducted a tree-plot analysis for pursuit and torsion in those blocks in Experiments 2 and 3, in which translational or rotational directions were randomized. In Figure 2.16, we show averaged eye velocities in trial  $n$  as a function of rotational (or translational) direction in the previous two trials ( $n-1$  and  $n-2$ ). If a priming effect existed for torsion, for example, we would expect eye velocity of trials preceded by a stimulus with CW rotation to be more positive than the averaged eye velocity of trials preceded by CCW rotation. We observed no systematic priming effect for either torsion in Experiment 2, or torsion or pursuit in Experiment 3, when averaging data across all participants. However, some individual observers' data reflect effects of priming. We conducted two-way ANOVAs (factor 1: direction of current trial; factor 2: direction of previous trial; test effect of factor 2) on individual observer data, revealing significant trial history effects for zero out of nine observers' torsion in Experiment 2, two out of five observers' torsion in Experiment 3, and zero out of five observers' pursuit in Experiment 3. However, given that the majority of observers did not exhibit trial history effects, and that the overall magnitude of anticipatory torsion was very small, it is unlikely that priming played a significant role in driving anticipatory eye movements in these two experiments.

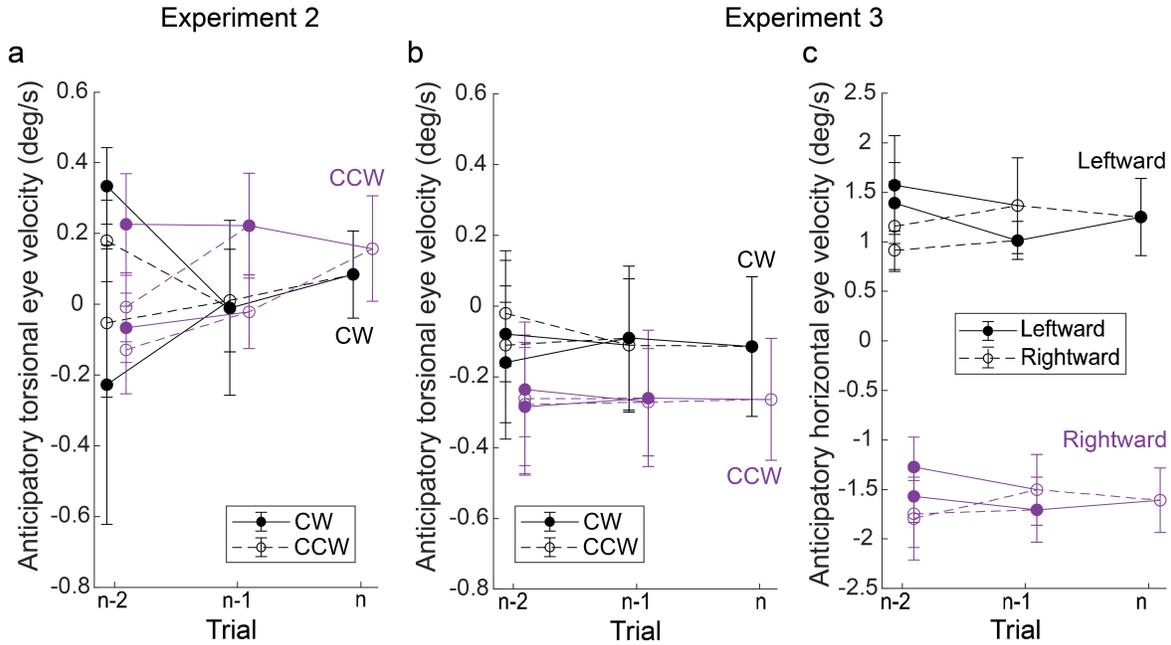
## 2.2.4 Discussion

In 1989, Eileen Kowler published a seminal article in which she demonstrated convincingly that “anticipatory smooth eye movement depended on both the cognitive expectations about the direction of future target motion and on the recent past history of stimulus motions” (Kowler 1989; p. 1055). Kowler's early findings attributed anticipatory pursuit to cognitive expectations, showing that simple oculomotor learning was insufficient to explain smooth movements of the eye prior to target motion onset. These results had significant ramifications for how we view smooth pursuit eye movements: not only as the retinal-slip driven visual response tightly linked to low-level motion processing, but also as a sensitive read-out of higher-level cognitive processes, such as predictive motion signals (Barnes and Collins, 2008; Kowler, 2011; Kowler et al., 2014).



**Figure 2.15:** Cumulative anticipatory eye velocities across observers (panels a-d show averages for  $n = 9$ , panels e and f show averages for  $n = 5$ ). (a, c, e) Anticipatory horizontal eye velocity in Experiments 1, 2 and 3. (b, d, f) Anticipatory torsion in Experiments 1, 2, and 3.

Here, we show that anticipatory ocular torsion can be elicited prior to the onset of a moving and rotating visual stimulus. However, whereas anticipatory pursuit was elicited reliably across experiments employing different cue strengths, anticipatory torsion was only triggered if the same pattern of rotational motion was presented repeatedly. This anticipatory response is therefore more likely to be driven by low-level learning or adaptive processes, and not by higher-level cognitive processes. Symbolic cues, such as arrow cues



**Figure 2.16:** The effect of previous trials on torsional anticipatory eye velocity when rotational or translational directions were randomized. The knot for trial  $n$  represents averaged eye velocity across all trials in which the stimulus rotated in a given direction (CW: black; CCW: purple) or translated in a given direction (left: black; right: purple). Moving to the left along the x axis, the two knots for trial  $n-1$  show the averaged eye velocity of trials split by the direction of the preceding trial, and so on. (a) Mean anticipatory torsion in Experiment 2 ( $n = 9$ ). (b) Mean anticipatory torsion and (c) mean anticipatory horizontal pursuit in Experiment 3 ( $n = 5$ ). Error bars denote standard error of the mean.

(Experiment 2) or barrier cues (Experiment 3) indicating an upcoming direction, require conscious higher-level decoding of the cue's meaning—a cognitive process that appears to be decoupled from the control of ocular torsion. The cues' differential potential in driving anticipatory pursuit and torsion indicates that these two types of anticipatory responses are at least partly decoupled and controlled separately.

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

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

Our results are consistent with the view that torsional eye movements are not purely reflexive or the mere byproduct of a gaze shift, as originally indicated by Donders' and Listing's law. Instead, torsion might be susceptible to learning or adaptation to a given rotational motion direction. Yet, in comparison with anticipatory horizontal pursuit, anticipatory torsion does not seem to be under much cognitive control. Anticipatory smooth pursuit is commonly associated with activity in frontal brain areas, such as the frontal eye fields (Fukushima et al., 2002; Macavoy et al., 1991), and in particular with the supplementary eye fields (Heinen and Liu, 1997; Missal and Heinen, 2004). However, there is no direct evidence that signals from these frontal cortical brain areas directly mediate the descending signals to the brainstem and cerebellum that are well-known to guide ocular torsion.

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

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

## **Limitations**

The interpretation of our findings is limited by several factors, most notably by the small magnitude of the

movement under study, and by the overall small effect sizes, even when anticipatory torsion was elicited in Experiment 1. Because of this, some experimental manipulations are not feasible. For example, it would be interesting to present moving stimuli with completely randomized translational and rotational motion directions, without a cue, to examine the isolated effects of trial history as has been done in the past for anticipatory pursuit (Heinen et al., 2005; Kowler, 1989). Yet, even a highly salient barrier cue did not reliably trigger anticipatory torsion in our experiments, rendering it unlikely that anticipatory torsion would survive complete randomization.

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

### **Conclusion**

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

## Chapter 3

# Tracking and perceiving diverse motion signals: different but related directional biases in human smooth pursuit and perception

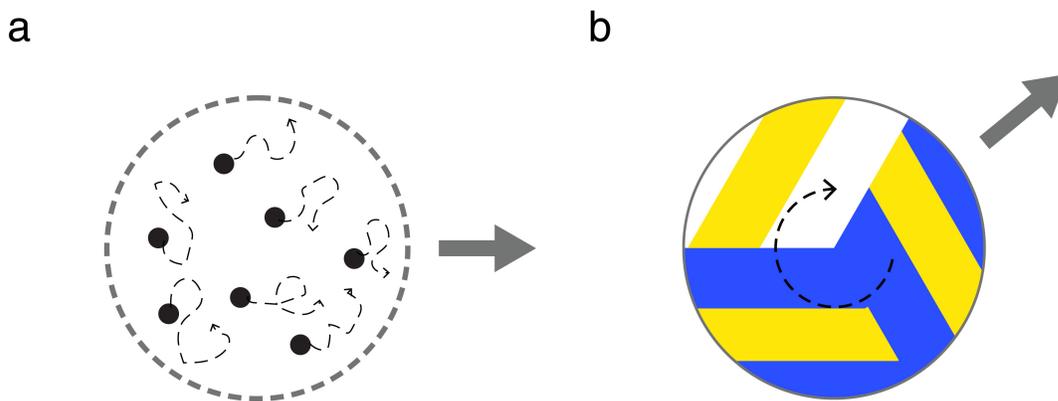
In the previous chapter, we have shown that visually-induced torsion is related to perception, but not under as much cognitive control as smooth pursuit. The tight link between motion perception and smooth pursuit is well known (Schütz et al., 2011; Spering and Montagnini, 2011), and often studied with simple stimuli such as a small dot translating across a blank screen. In this study, we examine the responses of and correlation between perception and smooth pursuit under a more complex situation, when motion signals across different spatial scales need to be processed.

### 3.1 Introduction

Living in a dynamic visual environment requires awareness of moving objects around us and the ability to rapidly evaluate and judge their direction and speed. In order to keep track of the moving objects around us, humans use smooth pursuit eye movements. This type of smooth, slow rotation of the eyes allows the continuous projection of an object of interest close to the fovea, the small area on our retinae that enables high visual acuity (Jacobs, 1979). Smooth pursuit eye movement is one of brain's key responses to visual motion and can only be initiated if an observer perceives motion (Steinbach, 1976). It is difficult to initiate a smooth response to non-visual motion signals, such as during auditory, tactile, or somatosensory stimulation (Berryhill et al., 2006). Whereas illusory motion can be tracked (Braun et al., 2006; Lorenceau, 2012), pursuit in the complete absence of a stimulus is not usually possible.

It appears to follow logically that this type of eye movement should be tightly linked to how we perceive

visual motion. Indeed, several studies have shown an association between both responses (for reviews, see Schütz et al. 2011; Spering and Montagnini 2011). For example, both perception and pursuit show similar accuracy and variability in direction and speed discrimination tasks (Gegenfurtner et al., 2003; Mukherjee et al., 2015; Osborne et al., 2005; Stone and Krauzlis, 2003). These perception-action associations are usually described under laboratory conditions that involve sparse visual stimuli, such as the translating motion of a single dot or static pattern (Gegenfurtner et al., 2003; Mukherjee et al., 2015; Osborne et al., 2005; Stone and Krauzlis, 2003). However, in daily life we usually encounter moving objects that contain additional internal motion signals (Fig. 3.1). For example, when we observe a swarm of insects, each insect inside the swarm has its own individual motion direction, yet the swarm also follows an overall (global) motion direction (Fig. 3.1a). Individual motion and global object motion occur on different spatial scales. Even for a single object such as a flying and rotating volleyball (Fig. 3.1b), object components (ball stripes) might present different motion signals from the global object motion.



**Figure 3.1:** Illustration of motion signals on different spatial scales. (a) Simple illustration of stimuli such as a swarm of insects. (b) Flying and rotating volleyball. The grey solid arrow indicates the object motion which operates on a larger spatial scale, and the black dashed arrows indicate the additional internal motion within each object, which is different from the object motion and operates on a smaller spatial scale.

Here, we investigate whether the assumed association between perception and pursuit extends to situations in which potentially diverse visual motion signals have to be processed across space. More specifically, we ask whether the internal motion of an object affects how we perceive and track its trajectory. This question is important because the processing of motion signals across space is a necessary prerequisite in order to derive an object’s veridical motion for accurate perception and pursuit in a more complex natural environment.

Whether this signal processing results in similar or different behavioural outcomes appears to depend on the stimulus environment and task. Evidence for perception-pursuit associations comes from studies employing objects that contain ambiguous local (internal) motion signals. A typical example is the “aperture

problem”, in which the object’s motion can only be decided if it is revealed or perceived in its entirety. Imagine a diagonally tilted bar translating horizontally and viewed through an aperture that covers the ends of the bar. Due to its orientation, the translation could be seen as either diagonal or horizontal. The ambiguity can only be resolved when the whole bar is visible. In this case, motion signals from local edges, such as the middle part of the stimulus, have to be combined with motion of structures, such as the ends of the stimulus, to inform its veridical direction. Perception and pursuit show a similar temporal development of directional biases in response to the aperture problem: perceived direction (Lorenceanu et al., 1993) and smooth pursuit direction (Bogadhi et al., 2011; Masson and Stone, 2002; Montagnini et al., 2006) are initially both biased to the local motion direction. These biases are then corrected toward the object motion direction after further integration of motion signals. When viewing segments of line-figure objects behind apertures (e.g., only the middle part of the four edges of a diamond shape is visible), direction perception and pursuit of the object motion are affected similarly by whether apertures are visible or not, which affects the degree to which an object is perceived as a whole rather than as individual line segments (Beutter and Stone, 2000; Stone et al., 2000). In sum, perception and pursuit seem to follow the same representation of object motion.

Evidence for perception-pursuit dissociations in motion signal processing comes from studies that require the assessment of the relative relationship between different motion signals. Motion signals at different spatial scales may not only come from within the object, but can also be associated with a small object moving against a large background. For example, when observers were asked to judge the speed of a small target in the presence of a large moving background, the perceived velocity of the target increased with decreasing context velocity (Spering and Gegenfurtner, 2007b). By contrast, pursuit velocity increased with increasing background speed (Lindner et al., 2001; Schwarz and Ilg, 1999; Spering and Gegenfurtner, 2007a,b). When the different motion signals are both within the target (a translating and drifting grating), a dissociation was found between speed perception and pursuit velocity (Hughes, 2018). No consistent bias was found in perceived speed, whereas pursuit velocity followed the average speed of the translating and drifting motion.

In sum, when observers judge an object’s direction by integrating diverse motion signals within an object, perception and pursuit tend to be associated. Both are affected by object and internal local motion. By contrast, when observers judge an object’s speed when the relationship of the diverse motion signals (within an object or between an object and its surround) needs to be determined, perception and pursuit tend to be dissociated. Pursuit is always affected by all diverse motion signals, whereas perception is either affected in the opposite direction to pursuit (Spering and Gegenfurtner, 2007b), or is not affected consistently (Hughes, 2018).

In the current study, we focus on object direction and investigate how the object’s internal motion direction and its global motion direction are processed to drive perception and pursuit of global object motion. Human observers viewed a random-dot kinematogram (RDK) translating across the screen, while constant dot motion inside the RDK was shown. We expect that pursuit will be biased toward the internal motion direction, and that it will reflect average direction signals from both sources (motion assimilation). Congruent with studies that report perception-pursuit associations (Beutter and Stone, 2000; Stone et al., 2000),

perception could be similarly biased by internal motion direction as pursuit, and follow a motion assimilation effect. This finding would imply that perception and pursuit use the same strategy to process object and internal motion. Alternatively, perception could follow a motion contrast effect (bias against the internal motion direction), as described in studies finding dissociations (Spering and Gegenfurtner, 2007b). A dissociation between perception and pursuit would indicate that different strategies are used by the two systems to process object and internal motion. We further examine whether biases in perception and pursuit are correlated across observers and within observers, which would indicate to what extent both responses are related. Whereas an across-observer correlation indicates an overall link in perception and pursuit, a trial-by-trial correlation indicates that they also share noise sources that commonly affect variability in sensorimotor responses (Osborne et al., 2005; Stone and Krauzlis, 2003). Our results will further our understanding of how perception and pursuit are related under more complex and ecologically valid situations.

## 3.2 Methods

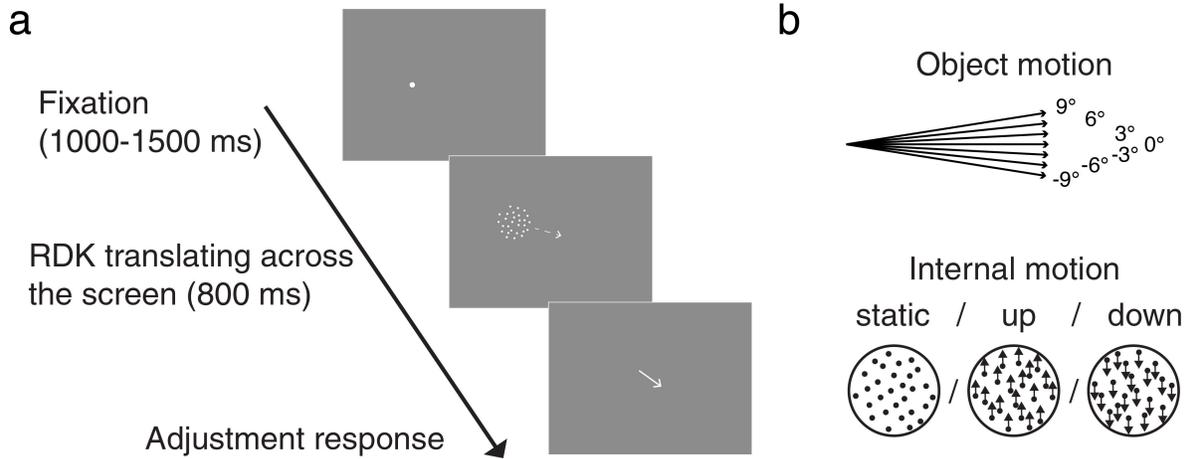
### Observers

We recruited 20 observers (age  $M = 26.75$ ,  $SD = 3.42$  years; nine female and 11 male) with self-reported normal or corrected-to-normal visual acuity and no history of ophthalmic, neurologic, or psychiatric disease. The sample size was determined by an a priori power analysis using G\*Power (Faul et al., 2007), and was suggested to be sufficient to detect an effect size of Cohen's  $f = 0.25$  and power of 0.85 for statistical tests (ANOVA) conducted to test our hypotheses. A medium effect size of 0.25 (Cohen, 1988) was chosen since Hughes (2018) found a large effect on pursuit (Cohen's  $f = 2.21$ , calculated based on Equation 13 from Lakens 2013), but perception showed no effect. The University of British Columbia Behavioural Research Ethics Board approved all experimental procedures, and all observers participated after giving written informed consent. Observers received \$10 CAD remuneration for each hour they participated in the experiment.

### Visual stimuli and setup

Stimuli were random-dot kinematograms (RDK) presented in an aperture with a radius of  $1^\circ$ . Each RDK consisted of 31 uniformly distributed white dots at a density of 10 dots/deg<sup>2</sup> and presented at a luminance of 52.86 cd/m<sup>2</sup> on a grey background (13.87 cd/m<sup>2</sup>). The whole RDK (aperture + dots) moved across a computer screen at a constant speed of 10°/s. We refer to this motion as the object motion. The object moved horizontally to the right, and at one of seven angles relative to horizontal, either at no deviation ( $0^\circ$ ) or oriented downwards ( $-9^\circ$ ,  $-6^\circ$ ,  $-3^\circ$ ) or upwards ( $3^\circ$ ,  $6^\circ$ , or  $9^\circ$ ; see Fig. 3.2b). Dots shown within the RDK were either stationary (baseline), or moved coherently at a constant speed of 5°/s in the upward ( $90^\circ$ ) or downward ( $-90^\circ$ ) direction relative to the aperture (Fig. 3.2b). The absolute dot velocity on the screen depended on the angle between the object and internal motion directions. The spatial displacement ( $\Delta x$ ) per frame was 7 to 8 arcmin (4 to 5 pixels). The duration of each frame ( $\Delta t$ ) was approximately 12 ms, at the rate equal to the screen refresh rate of 85 Hz. Dot lifetime was nine frames (approximately 106 ms). Each dot

was initialized with a random duration of lifetime left, in order to avoid a whole-RDK flash when replacing the expired dots. At the end of its lifetime, a given dot reappeared at a random location within the aperture. When a dot moved out of the aperture, it re-entered from the opposite side of the aperture.



**Figure 3.2:** (a) Trial timeline and (b) object and internal motion direction. At the beginning of each trial, a fixation point was shown for 1000-1500 ms, followed by the RDK translating across the screen for 800 ms (dashed arrow is for illustration purposes and was not shown in the experiment). A response arrow was shown after the RDK until observers clicked the mouse button to submit their response.

Observers were seated in a dimly-lit room and viewed all stimuli on a gamma-corrected  $36.7 \text{ cm} \times 27.5 \text{ cm}$  CRT monitor (ViewSonic G90fB; resolution  $1280 \times 1024$  pixels; refresh rate 85 Hz). The viewing distance was 55 cm. Each observer's head was stabilized using a chin-and-forehead-rest. Stimuli and procedure were programmed in MATLAB R2019a (The MathWorks Inc., Natick, MA) and Psychtoolbox Version 3.0.12 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

### Procedure and design

Each block of trials started with a standard 5-point calibration of the eye tracker. Each trial then started with a white fixation point which observers were asked to fixate until it disappeared after 1000-1500 ms (Fig. 3.2a). Fixation was monitored online: if eye position was further than  $1^\circ$  from the centre of the fixation point, the fixation point turned red and the countdown of fixation duration was paused until the observer regained accurate fixation. After fixation, we used an adapted step-ramp paradigm: the RDK appeared slightly backward on its motion trajectory to the left of the fixation location, and then moved rightward along its motion trajectory. Such a step-ramp paradigm is typically used to prevent the initial use of saccades and instead elicit a smooth initiation of pursuit to the target (Rashbass, 1961). The RDK moved across the screen for 800 ms, and observers were asked to follow the object motion as smoothly as possible with their eyes. After the RDK disappeared, a white response arrow appeared at the screen centre. Observers were instructed to report the object motion direction by adjusting the angle of the arrow using the

track-ball mouse (the arrow would always point to the cursor position) and then click the mouse button to submit the response. There was no time pressure for responding, and no feedback was given. To ensure that observers did not use location as a cue by simply pointing the arrow to the final location of the RDK, the object motion trajectory contained spatial jitter. The middle (half-way) point of the object motion trajectory was by default at the screen centre; the addition of the spatial jitter resulted in a random placement of the half-way point within  $1^\circ$  of the screen centre. This spatial randomization was explained to the observers, and they were strongly encouraged to focus on the angle of the object motion trajectory instead of using the last location of the RDK as a reference.

The manipulations of trajectory angle and internal motion results in a  $7$  (angle)  $\times$   $3$  (internal motion) within-subject design. Each experimental block consisted of 42 trials, with 2 trials per condition, all randomly interleaved. Observers first performed one practice block of 21 trials (one trial per condition) to get familiar with the task, and then completed 10 experimental blocks. Data from the practice block were not analyzed. Including breaks between blocks, the experiment took between 50 and 75 minutes.

### **Eye movement recording and analysis**

The position of the right eye was recorded at a sampling rate of 1000 Hz using a video-based eye tracker (EyeLink 1000 tower-mount, SR Research Ltd., Kanata, ON, Canada). Eye movements were then analyzed offline using custom-made MATLAB functions. Eye position, velocity, and acceleration data were filtered with a second-order Butterworth filter (cutoff frequencies of 15 Hz for position and 30 Hz for velocity and acceleration). Eye direction was calculated as the angle of the velocity vector, represented in the same way as object motion direction (horizontal right is  $0^\circ$ , and counterclockwise is positive). Trials with blinks during RDK presentation or trials with signal loss were manually labelled as invalid and excluded (5 on average across observers). We also excluded trials in which the perceptual report was to the left ( $<0.2$  across observers).

Saccades were detected based on an acceleration criterion: the acceleration trace was segmented by zero-crossing points, and peak acceleration within each segment was calculated. If at least two consecutive segments had absolute peak acceleration larger than  $400^\circ/s^2$ , these segments were defined as saccades. An acceleration threshold was used to accurately detect saccades of small amplitude and velocity. Saccade detection was confirmed by visual inspection of the velocity traces in each trial. Saccades were excluded from the analysis of smooth pursuit.

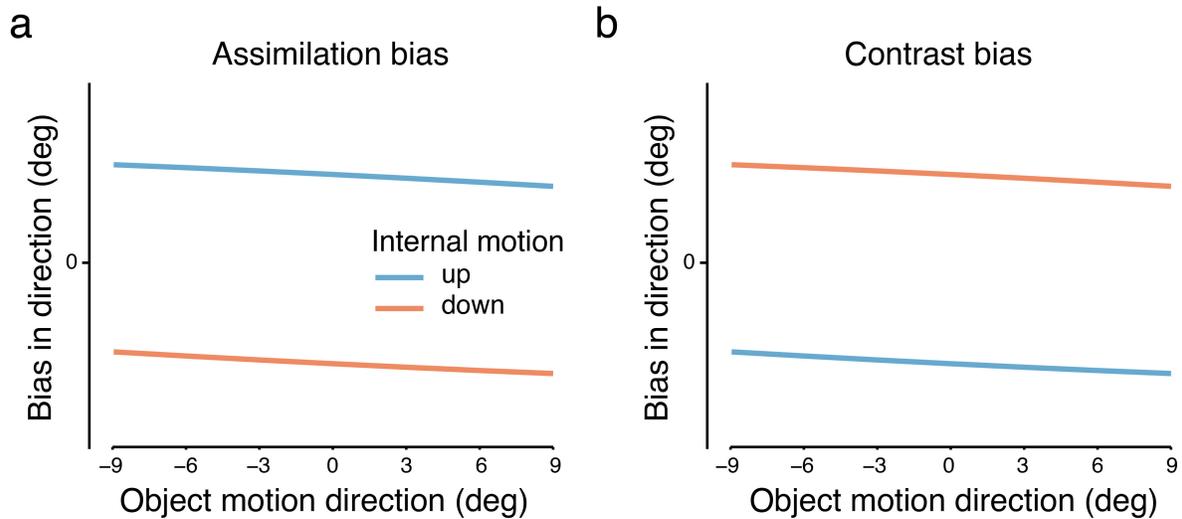
Smooth pursuit onset was detected in each trial by fitting a piecewise linear function with two segments and a break point (as previously reported in Rothwell et al. 2020) to the filtered and saccade-interpolated velocity traces (eye positions were linearly interpolated between saccade onsets and offsets). The fitting window to detect pursuit onset started at RDK onset, and the end of the window was 150 ms after the point at which eye velocity consistently exceeded four times the standard deviation of the fixation noise (Blohm and Lefèvre, 2010). We calculated the averaged pursuit direction during the steady-state phase, defined as the time period between 140 ms after pursuit onset to 100 ms before the end of the visual motion display. We excluded the last 100 ms due to known anticipatory slowing of the eyes.

## Hypotheses and statistical analysis

We aim to test the following hypotheses. First, we expect that pursuit direction will be biased toward the internal motion direction, showing a bias in the average motion direction (motion assimilation; Fig. 3.3a). Second, we expect that perceived direction will be affected by internal motion. It could either show a similar assimilation bias as pursuit (Fig. 3.3a), or alternatively, it could be biased against the internal motion direction (motion contrast; Fig. 3.3b). To test these hypotheses, we calculated directional bias as the difference between tracked/perceived direction in the internal-motion conditions and the baseline condition with no internal motion (static dots inside the RDK). To assess whether perception and pursuit followed motion assimilation—the average between the internal and the object motion directions—or contrast—the difference between internal and object motion directions, we used two-way repeated measures of analysis of variances (rmANOVA). Perceived or pursuit bias is the dependent variable, and *internal motion* (upward/downward) and *object motion* (seven angles,  $-9^\circ$ ,  $-6^\circ$ ,  $-3^\circ$ , or  $0^\circ$ ) are within-subjects factors. A significant main effect of *internal motion* would indicate a bias. The direction of this main effect would then indicate the type of bias: an assimilation bias describes a bias in the same direction as internal motion, i.e., an upward trend in perception and pursuit in response to upward internal motion and a downward trend in response to downward internal motion (Fig. 3.3a), whereas a contrast bias is indicated by the opposite pattern (Fig. 3.3b). A significant main effect of *object motion* is expected because averaging or contrasting object and internal motion would result in the bias values being more negative when object motion direction is more positive (negative slopes in Fig. 3.3). We do not expect any significant interaction effects of *internal motion*  $\times$  *object motion*, although one could be observed if perception or pursuit responded stronger to either upward or downward motion (e.g., Ke et al., 2013).

If perception and pursuit biases were related, we would expect to see a significant across-observer correlation. To examine this, we calculated the Pearson’s correlation coefficient between directional biases in perception and pursuit. For each observer, we averaged the bias across conditions so that all trials have an upward internal motion direction (a positive value would indicate bias in the same direction as internal motion). Further, if perception and pursuit shared noise sources during motion processing, we would expect to see a within-observer trial-by-trial correlation between perceptual and pursuit biases. To examine this, we fitted a linear mixed-effects model of perceptual bias with *object motion*, *internal motion*, and *pursuit bias* as fixed effects and with individual intercept and slope as random effects [formula: perceptual bias  $\sim$  object motion + internal motion + pursuit bias + (1 + pursuit bias | observer)]. A significant fixed effect of pursuit bias would indicate a significant trial-by-trial correlation.

We used an  $\alpha$ -error probability of 5% ( $p < 0.05$  is considered significant). For effect sizes, we report partial eta-squared ( $\eta_p^2$ ) in two-way ANOVAs. The statistical tests were conducted in R Version 4.1.2 (package "lme4", Bates et al. 2015; package "lmerTest", Kuznetsova et al. 2017; package "ez", Lawrence 2016; package "psychReport", Mackenzie and Dudschig 2021; R Core Team 2019) and MATLAB R2020a.



**Figure 3.3:** Hypotheses for (a) assimilation bias and (b) contrast bias. The plots show the pattern of averaging/contrasting the object and dot motion directions. The slope across object motion directions was simply due to the fixed speed and different relative angles between the object and internal motion. (a) If pursuit/perception followed the assimilation bias, the direction bias would be in the same direction as the internal motion direction. (b) If perception followed the contrast bias, then the direction bias would be in the opposite direction to the internal motion direction.

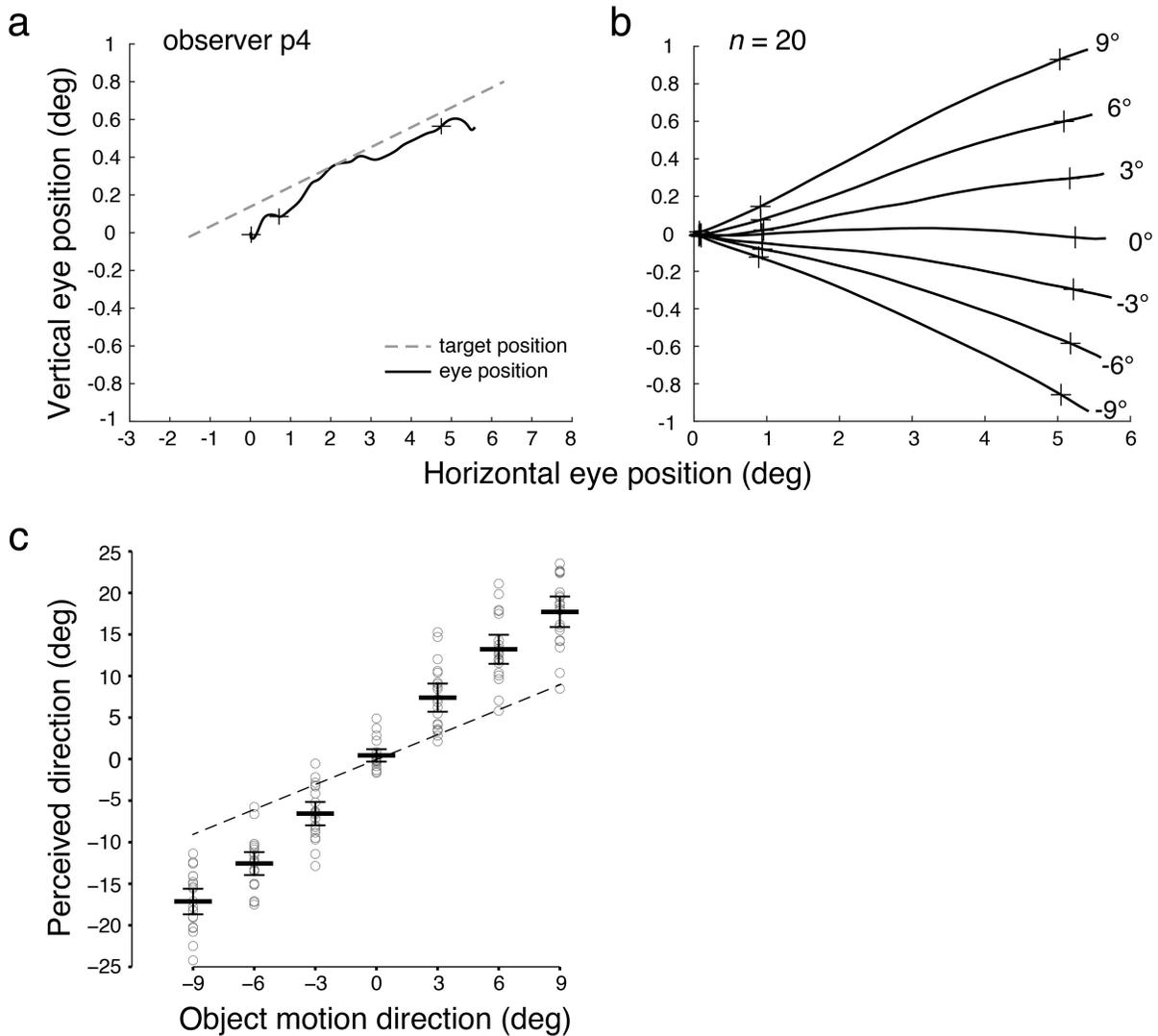
### 3.3 Results

#### Veridical perception and tracking of object motion in the absence of internal motion

In this study, we compared perception and pursuit in trials in which an object's motion direction was either combined or not combined with internal motion. Figure 3.4a shows an example eye position trace from one single trial for a representative subject in comparison to the target trajectory, and Figure 3.4b shows average eye position traces across observers in each object motion condition. Pursuit was initiated 132 ms ( $SD = 16$  ms) after target onset on average, and then followed the veridical object motion direction in trials in which there was no internal motion (baseline). Perceived direction roughly matched the object motion direction, with a general trend to overestimate (Fig. 3.4c). To examine the effect of internal motion direction on perceived and tracked object motion, we subtracted the baseline responses to calculate the perceptual and pursuit biases in trials with internal motion (upward/downward) and examined how the biases were affected by internal motion directions.

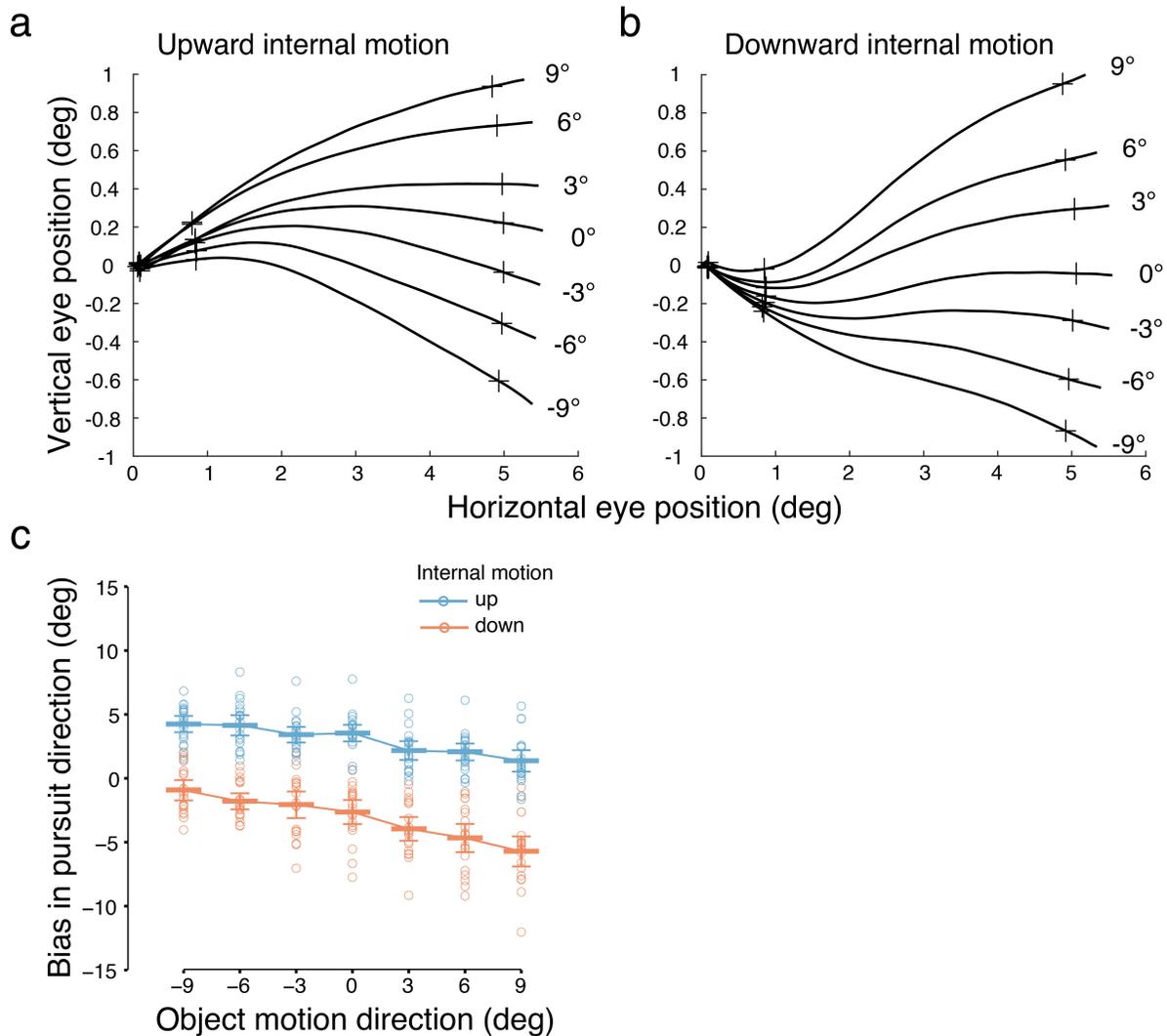
#### Assimilation bias in smooth pursuit direction

In trials in which object motion was combined with diverse internal motion signals (either upward or downward relative to horizontal), we observed that pursuit eye movements were biased toward the internal motion direction (Fig. 3.5, a, b). When internal dots moved upward, the eye was biased in the upward motion direction, and vice versa for downward motion. This assimilation bias was confirmed by a significant main



**Figure 3.4:** (a) Example eye position trace from one trial without internal motion from RDK onset to RDK offset. The object motion direction (dashed line indicates trajectory of RDK center) is  $6^\circ$ . From left to right, the crosses indicate time points of the pursuit onset, and the start and end of steady-state phase analysis window, respectively. (b) Average eye position traces across observers in the baseline internal motion condition. All traces are aligned to start from RDK onset at location (0, 0), and end at RDK offset. Numbers denote the object motion directions. (c) Perceived direction in the baseline condition averaged across observers ( $n = 20$ ). Horizontal bars indicate mean perceived direction across observers, and error bars indicate the 95% CI. The circles indicate the mean perceived direction of individual observers. The dashed line indicates the identity line. If the perceived direction was accurate without overestimation, data should fall on the identity line. CI, confidence interval.

effect of *internal motion* on pursuit [ $F(1, 19) = 167.88, p < 0.001, \eta_p^2 = 0.90$ ], with positive biases in the upward internal motion condition and negative biases in the downward motion direction (Fig. 3.5c). The assimilation bias pattern in pursuit was observed in all observers, as can be inferred from individual data points in Figure 3.5c, which fall into two separate clusters around the mean per internal motion direction.



**Figure 3.5:** Average ( $n = 20$ ) eye position traces for (a) upward and (b) downward internal motion. The crosses indicate time points of pursuit onset, and the start and end of the steady-state phase analysis window. Numbers note the object motion directions. (c) Bias in pursuit direction averaged across all observers ( $n = 20$ ). Horizontal bars indicate the mean across observers, and error bars indicate the 95% CI. The circles indicate the mean of individual observers. CI, confidence interval.

We also found a negative slope of pursuit bias across object motion conditions, shown by a significant main effect of *object motion* [ $F(6, 114) = 28.07, p < 0.001, \eta_p^2 = 0.60$ ]. Moreover, we observed an asymme-

try in pursuit bias with a larger bias in response to downward vs. upward internal motion direction. This observation was confirmed by a significant *object motion*  $\times$  *internal motion* interaction [ $F(2.94, 55.80) = 4.27$ ,  $p = 0.01$ ,  $\eta_p^2 = 0.18$ ]. In summary, pursuit eye movements are biased toward the internal motion direction, following a motion assimilation effect, consistent with our hypothesis (Fig. 3.3a).

### **Inconsistent bias in perceived direction**

Observers were asked to report the perceived direction of the RDK by adjusting a response arrow in the perceived direction. In contrast to the consistent bias in the average motion direction in pursuit, across all observers, perceived direction was not affected by internal motion direction (Fig. 3.6a). Congruently, the main effect of *internal motion* on perception was not significant [ $F(1, 19) = 0.57$ ,  $p = 0.46$ ,  $\eta_p^2 = 0.03$ ]. The negative slope of biases across object motion directions (Fig. 3.3) was still observed, shown by a significant main effect of *object motion* [ $F(3.57, 67.74) = 23.12$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.55$ ], but there was no up/down asymmetry in perceptual biases, indicated by a non-significant *object motion*  $\times$  *internal motion* interaction [ $F(2.81, 53.43) = 0.39$ ,  $p = 0.74$ ,  $\eta_p^2 = 0.02$ ]. In sum, our findings do not support a perceptual bias in either the average (assimilation) or relative (contrast) motion direction.

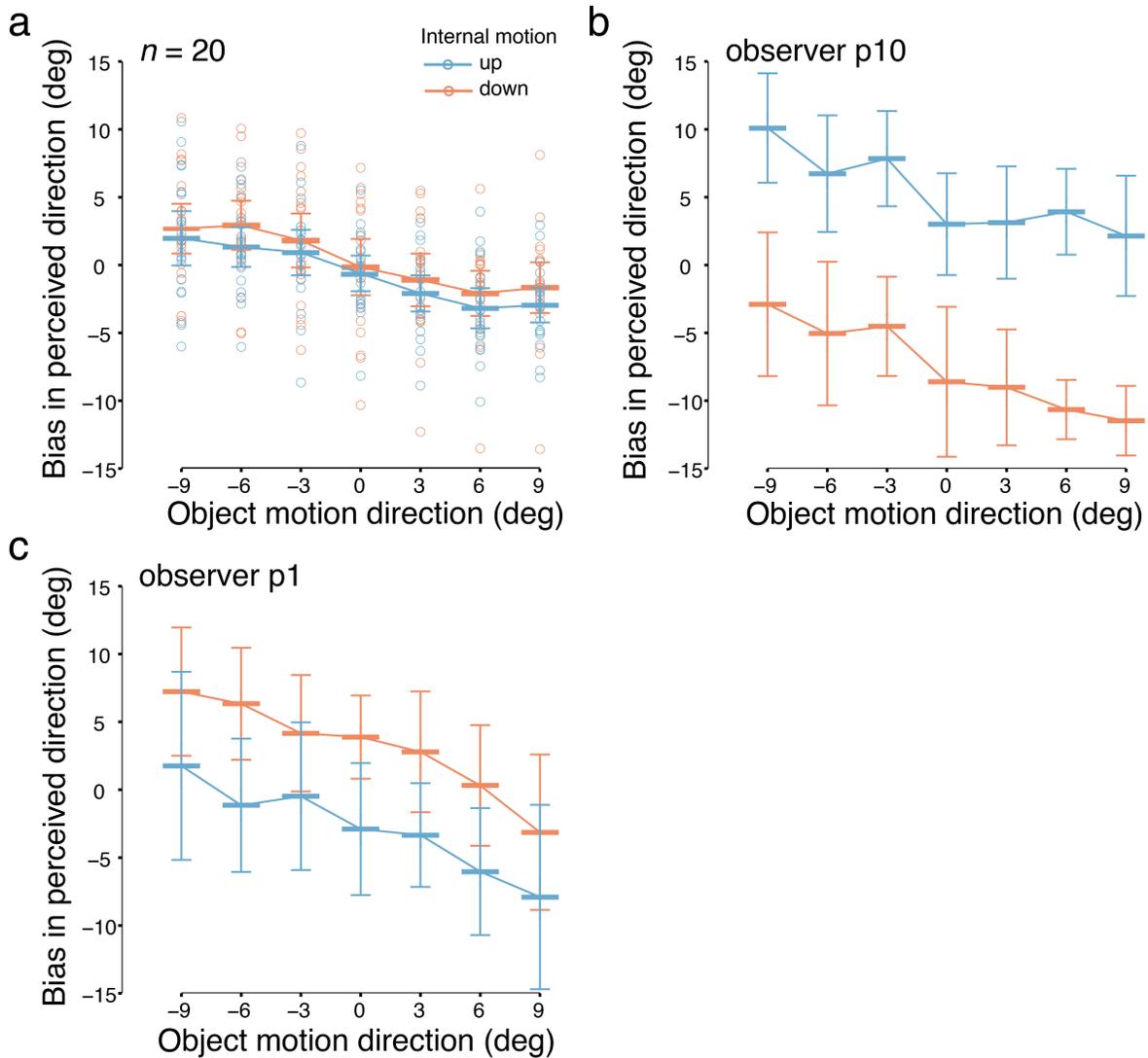
Further examination of individual data revealed a possible reason for the lack of perceptual bias in the group data. Whereas some participants showed an assimilation bias (Fig. 3.6b), other participants' perception was biased in the contrast motion direction (Fig. 3.6c). This may also explain why the negative slope of perceptual bias across object motion directions is preserved when averaging across observers, because the slope is similar in both assimilation and contrast biases. Detailed individual data and different perceptual bias patterns are described in the section on Exploratory Analyses (see below).

### **Correlation between perception and pursuit biases**

Results above show that whereas the tracking direction of the RDK in all observers was biased toward the internal motion direction, perceived direction was not biased on average. However, perception and pursuit could still share motion processing at a low level, and further process motion signals in different ways. If low-level motion processing is shared, we should see correlations between perceptual and pursuit biases, regardless of their diverse bias patterns. We conducted both across-observer and trial-by-trial correlations between perceptual and pursuit biases, to examine to what extent the two systems are related.

We found that even though perception and pursuit did not show similar response bias patterns, their directional responses were related, as indicated by a significant across-observer correlation ( $r = 0.75$ ,  $p < 0.001$ ; Fig. 3.7). These findings imply that participants with a larger pursuit bias in the direction of internal motion tended to also have a larger perceptual bias in the direction of internal motion. By contrast, participants with a smaller pursuit bias tended to exhibit a perceptual bias toward the motion contrast direction.

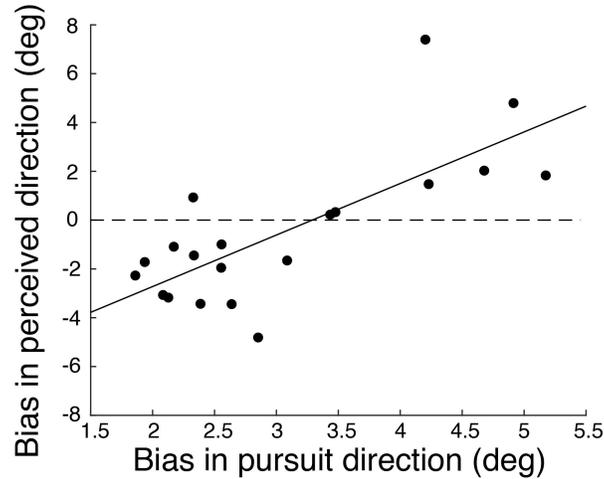
To further examine whether internal noise in the motion processing systems is shared between perception and pursuit, as would be indicated by significant trial-by-trial correlations which signify that the variability of the responses is related, we fitted a linear mixed effects model. We did not find significant trial-by-trial correlations, indicated by a non-significant fixed effect of *pursuit bias* on perceptual bias [estimate  $\pm$  95%



**Figure 3.6:** (a) Biases in perceived direction averaged across all observers. Horizontal bars indicate the mean across observers, and error bars indicate the 95% CI. The following panels show examples of individual data showing (b) assimilation bias or (c) contrast bias in perception. Horizontal bars indicate the mean perceived direction bias across trials, and error bars indicate the standard deviation. CI, confidence interval.

CI =  $0.06 \pm 0.15$ ,  $t(21.11) = 0.80$ ,  $p = 0.43$ ]. This suggests that perception and pursuit are unlikely to share sensory or motor noise sources in this particular task.

Overall, our results point at a dissociation of response patterns between perception and pursuit. Whereas the perceptual bias was inconsistent across observers, pursuit was consistently biased toward the internal motion direction. Notwithstanding these differences, perceptual and pursuit biases were correlated across observers. Participants with larger assimilation bias in pursuit tended to have an assimilation bias in percep-



**Figure 3.7:** Correlation between the bias in perceived direction and the bias in pursuit direction across observers ( $n = 20$ ). Each data point indicates the average value between internal motion conditions for one observer (positive values indicated bias in the direction of internal motion). The solid line shows the least squares fit. The dashed line indicates zero perceptual bias.

tion, whereas participants with smaller pursuit biases tended to exhibit a contrast bias in perception. In the following section, we will report exploratory analyses to further examine potential subgroups of participants with different perceptual biases.

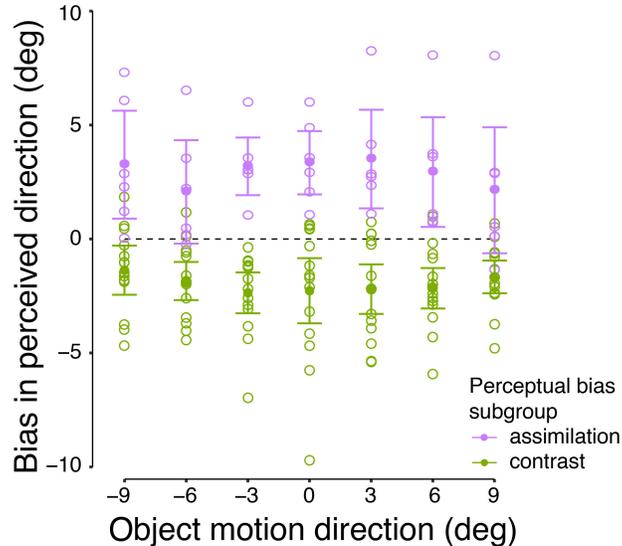
### Exploratory analyses on individual differences

We hypothesized that perception would either show an assimilation bias similar to pursuit, or a contrast bias different from pursuit. However, the overall perceptual bias across observers showed no effect of internal motion (Fig. 3.6a). Individual data implied that people might differ in how their perception was biased (Fig. 3.6, b, c), thus resulting in an overall null result. The scatter plot in Figure 3.7 shows that the majority of data points falls in the lower left quadrant, with a relatively small pursuit bias and a contrast bias in perception. However, some data points fall in the upper right quadrant, revealing a strong pursuit bias and an assimilation bias in perception that is congruent with the pursuit result; other data points cannot be classified into either of these groups.

To investigate this clustering, we performed a latent profile analysis on perceptual bias across observers. Latent profile analysis uses maximum likelihood estimation to identify heterogeneous subgroups with different patterns of variables measured (Harring and Hodis, 2016; Peugh and Fan, 2013; Spurk et al., 2020). In our case, the measured variables are the perceptual bias across object motion conditions, and the patterns are assimilation vs. contrast. We calculated the bootstrapped mean (of 1000 simulations) for each *object motion*  $\times$  *internal motion* condition in each observer, then averaged the perceptual bias between internal motion conditions (conditions were merged so that internal motion was upward in all trials). Each observer had seven perceptual bias values, one for each object motion condition. Assimilation bias corresponds to

positive values, and contrast bias corresponds to negative values. A latent profile analysis was performed with the assumption of two subgroups (analysis was done using R package "tidyLPA", Rosenberg et al. 2019). The latent profile analysis does not prove the existence of subgroups, but allows us to explore the results if this assumption was true.

The algorithm was able to classify observers into two groups reliably, indicated by high probability of group classification ( $M = 98.91\%$ ,  $SD = 1.63\%$ ). Figure 3.8 shows perceptual bias patterns for the two subgroups, an assimilation group ( $n = 6$ ) and a contrast group ( $n = 14$ ). Each group showed the expected perceptual bias patterns with significant main effects of *internal motion* [assimilation:  $F(1,5) = 9.05$ ,  $p = 0.03$ ,  $\eta_p^2 = 0.64$ ; contrast:  $F(1,13) = 27.63$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.68$ ]. These findings indicate potential individual differences in perception that appear to be related to the strength of the pursuit bias. Further exploratory analyses were performed to examine how pursuit biases between perceptual subgroups change over time, and how the net motion energy of retinal images change over time due to eye movements, see Appendix. Motion energy provides an estimation of the neural activities encoding visual motion in the middle temporal area (area MT; Adelson and Bergen 1985; Kiani et al. 2008), and might indicate how perception could be affected. In general, we found that the difference in pursuit bias between perceptual subgroups only emerged in late steady-state pursuit (Fig. A. 1). In addition, net motion energy of retinal images during smooth pursuit was in the opposite direction to internal motion (Fig. A. 2). These findings provide additional insights in the interpretation of the across-observer correlation between perception and pursuit, and individual differences in perception, see Discussion.



**Figure 3.8:** Perceptual bias patterns analyzed in the latent profile analysis. The assimilation and contrast bias patterns are marked by colour and shape. Open circles indicate the individual bootstrapped mean of perceptual bias in one object motion condition. Filled circles indicate the average perceptual bias within each subgroup. Error bars indicate the 95% CI. CI, confidence interval.

### 3.4 Discussion

In this study, we examined how perception and pursuit process motion signals within an object and integrate them with object motion signals. Whereas smooth pursuit eye movements consistently followed the average of internal and object motion, perceptual biases were inconsistent across observers. Most observers showed a contrast bias in perception, but a few observers showed an assimilation bias. Interestingly, biases in perception and pursuit were correlated, showing that observers with a larger assimilation bias in pursuit tended to have a similar assimilation bias in perception. These results reveal a complex relationship between direction perception and smooth pursuit when processing motion signals at different spatial scales.

Different motion signals across space in the current study either associated with the whole object translating across the screen, or with internal object motion. This introduces ambiguity with regard to how to interpret the relationship between different motion signal sources. Our findings are in line with previous studies showing dissociations between perception and pursuit under similarly complex motion conditions. When perception and pursuit are faced with diverse motion signals from target and background (Spering and Gegenfurtner, 2007b) or from object and internal stripes (Hughes, 2018), perception and pursuit are biased by background or internal motion in different ways. Whereas perception followed the relative difference between target and background speed, or showed no bias toward internal motion on average, pursuit always followed the vector average of all available motion signals. These different biases may reflect different functional demands of perception and pursuit.

Perception needs to recognize and classify visual information, thus segregating the target from its context (Roelfsema, 2006; Roelfsema et al., 2002). Therefore, when the target is surrounded by a large-scale background, perception follows the relative speed between target and background (Spering and Gegenfurtner, 2007b). When diverse motion signals occur all within the target, as in the current study, perception tends to show no bias overall. Observers in our study might not have consistently regarded internal motion as part of the scene from which the object motion had to be segregated. Individual differences in perceptual bias patterns might suggest that different observers either segregated or integrated object and internal motion (Fig. 3.8). These differences are potentially due to different interpretations of whether the internal motion contributes to object motion or not. We will discuss additional reasons for individual differences in perception, and their implications, in the next section. Conversely, pursuit integrates all available motion signals in order to maximize the ability to monitor and collect information from the whole scene, resulting in an assimilation bias.

Studies have shown that different strategies—segregation and integration—can be used in parallel. When embedding a single, moving target dot within an RDK, the direction discrimination threshold of either the local (target dot) or the global (all background dots in the RDK) motion was not affected by whether observers were told to discriminate local or global motion beforehand (Watamaniuk and McKee, 1998). This suggests that local and global motion directions were processed simultaneously, and that participants had access to both. During a dual task, in which observers were asked to attend to an individual dot within a group of dots while using their eyes to track the motion of the group, performance in both tasks

was as good as when performing each task alone (Jin et al., 2014). These studies indicate that segregation and integration can be performed simultaneously, potentially serving the different functional demands of perception and pursuit.

Our findings are different from studies showing an association between perception and pursuit when integrating ambiguous local motion signals (Beutter and Stone, 2000; Stone et al., 2000). In these studies, a line-figure object was only partially visible through an aperture, and observers were asked to track the object and report its motion direction. In this case, the local motion signals simply needed to be integrated to derive object motion. Therefore, unlike in the current study, there was neither a conflict between internal and object motion signals, nor ambiguity in how to interpret their relationship. Instead, both perception and pursuit relied on a coherent representation of the object motion, resulting in response similarity.

### **Individual differences in perception but not pursuit**

An interesting dichotomy in perception and pursuit in the current study lies in the existence of individual differences in perception despite a consistent pursuit bias. Most observers (14 out of 20) showed a contrast bias, whereas some showed an assimilation bias. This individual difference in perception was also observed in a previous study comparing speed perception and pursuit velocity in response to translating and drifting gratings (Hughes, 2018). Congruently, Spering and Gegenfurtner (2007b) found larger variance in the correlation of perceptual responses with a model prediction of motion contrast than in the correlation of pursuit with an assimilation prediction. Below, we will discuss two potential sources of ambiguity in the current study, which could drive the diversity in perception.

First, because we did not provide any instruction with regard to the internal motion in our stimuli, it is possible that observers had different interpretations of its relevance. Anecdotal conversations with observers suggest that some perceived the RDK as a ball rolling along a curved path, whereas others did not notice the internal dot motion. Therefore, some observers might have considered the internal motion as an intrinsic contributor to object motion, resulting in an assimilation bias, whereas others might have considered it as noise that should be either ignored or counteracted, resulting in a contrast bias. In order to track an object, the eyes need to integrate motion signals from all sources in order to continuously update motion information, and to respond to any potential object trajectory changes at short latency so that the object remains close to the fovea. Because the motion signals themselves are not ambiguous in the current study, pursuit averaged the available motion signals, mirroring results obtained in previous studies (Hughes, 2018; Spering and Gegenfurtner, 2007a,b).

In addition to the uncertainty in the interpretation of internal motion, the ambiguity in motion energy in our stimuli could also contribute to a diverse perceptual response. Reverse motion perception has been observed widely with RDK stimuli, and occasionally with sinusoidal gratings. A small number of observers (usually less than 15%) may consistently perceive motion in the opposite direction to the actual dot motion (Manning et al., 2022). Even with RDKs of 100% coherence, similar to the stimuli used in the current study, observers can still show reverse motion perception (Meier and Giaschi, 2014, 2017, 2019). The probability of perceiving the actual motion direction presented in an RDK, or the opposite or orthogonal direction,

corresponds to the relative strength of motion energy in all perceived directions (Bae and Luck, 2022). Even RDKs of 100% coherence could contain motion energy in the opposite direction, which might contribute to the reverse motion perception (Manning et al., 2022). The motion energy analysis for our stimuli shows that the net motion energy of retinal images along the vertical dimension was in the opposite direction to internal motion (Fig. A. 2), which could be a source of ambiguity in the direction signal. Although it is unlikely that the known reverse motion perception with RDK stimuli fully explains the individual differences observed here, it could contribute to task and stimulus uncertainty and enhance existing individual differences in perception.

In summary, several sources of uncertainty exist in the current task, including observers' interpretation of the task relevance of internal motion, and ambiguity in direction signals indicated by retinal motion energy. The need of the perceptual system to consider the context of the target might have resulted in discrepancies between observers in how object and internal motion should be processed. However, the pursuit system aims to monitor and collect information from the whole scene, thus performing signal integration irrespective of target-context interpretation.

### **Correlation between biases in perceptual and pursuit responses**

Notwithstanding the perceptual diversity and pursuit consistency, we found that biases in both responses were correlated across observers, but not on a trial-by-trial basis. This indicates that even when perception and pursuit responses are linked, they likely have largely separated noise sources (Rasche and Gegenfurtner, 2009). One possibility is that perception and pursuit share processing of low-level motion signals at an early stage, for example, in early visual cortical areas such as the primary visual cortex (V1) and MT. However, previous studies (Hughes, 2018; Spering and Gegenfurtner, 2007b) showing dissociations did not find correlations between perception and pursuit. Hughes (2018) found that the correlation between speed perception and pursuit velocity across observers was not significant. Spering and Gegenfurtner (2007b) did not directly test the correlation between perception and pursuit across observers, but showed that speed perception and pursuit velocity were independently modulated by the relative direction of target and background motion, i.e., whether the background was moving in the same or opposite direction to target motion. Importantly, these two studies focused on speed perception, whereas the current study assessed direction perception.

That the exact motion feature under scrutiny matters is revealed by comparing previous studies that either reported trial-by-trial correlations between direction discrimination and pursuit (Mukherjee et al., 2015; Osborne et al., 2005; Stone and Krauzlis, 2003), or did not report trial-by-trial correlations between speed discrimination and pursuit (Gegenfurtner et al. 2003; Rasche and Gegenfurtner 2009; but see Mukherjee et al. 2015; Osborne et al. 2005). Direction and speed information are processed together when observers view simple motion stimuli, such as sinusoidal gratings or random dots (Reisbeck and Gegenfurtner, 1999; Schrater and Simoncelli, 1998). However, direction and speed discrimination differ depending on whether a stimulus moves along the cardinal axes or diagonally (Matthews and Qian, 1999), and are learned independently through repeated practice of discrimination tasks (Saffell and Matthews, 2003). Direction and speed information are also used differently when hitting moving targets in interceptive hand movement tasks

(Brouwer et al., 2003). In addition, single-pulse transcranial magnetic stimulation only impairs speed discrimination but not direction discrimination of moving stimuli (Nemeth et al., 2001). These results indicate partially separate processing of direction and speed information potentially in V1 and MT (Huk and Heeger, 2000; Nemeth et al., 2001), which might explain why the correlation between perception and pursuit across observers could differ depending on whether direction or speed was tested.

Another interpretation could be that a top-down perceptual modulation on pursuit contributes to the correlation between perception and pursuit. By performing further exploratory analyses of the temporal dynamics in pursuit biases between perceptual subgroups (Appendix A. 1), we found that the differences in pursuit bias between subgroups only emerged in late steady-state pursuit, whereas both groups have similar pursuit biases during early pursuit phases. In addition, during the late steady-state phase, some observers of the contrast group even showed a pursuit bias in the opposite direction to the internal motion (Fig. A. 1b), similar to their perceptual biases. It has been suggested that a perceptual decision could be formed during the stimulus display once enough evidence has been accumulated. When a perturbation of motion coherence of the RDK stimulus was introduced at a random time within a trial, perceived direction was biased more by the coherence perturbation when it was presented earlier than later in the trial (Kiani et al., 2008). By comparing discrimination thresholds from data and theoretical discrimination thresholds calculated based on the assumption of perfect integration of all stimulus information presented, the authors proposed that the perceptual system might have made a decision earlier during stimulus display (about 400 ms after stimulus onset in this task) and not fully utilized the later stimulus information (Kiani et al., 2008). It is possible that in the current study later pursuit was more aligned with perception once the perceptual decision was formed.

### **Neural correlates**

Different biases in perception and pursuit might reflect dependency on different types of MT neurons. Neurophysiological studies have revealed that MT neurons exhibit inhibitory or excitatory center-surround receptive fields, responding to either small-scale or large-field motion (Allman et al., 1985; Born, 2000; Born and Tootell, 1992; Tanaka et al., 1986). Activities of these MT neurons might be responsible for segregation and integration of motion signals, respectively (Andersen, 1997; Born and Bradley, 2005). Whereas perception might rely on the activities of MT neurons with inhibitory center-surround receptive fields to perform object segregation, pursuit might rely on the activities of MT neurons with excitatory center-surround receptive fields that spatially sum over larger regions of the visual field and average motion signals. In general, the different response patterns of perception and pursuit in the current study might indicate that motion processing for perception and pursuit separate at the level of MT.

### **Limitations and future directions**

In this study, we showed different but related perception and pursuit responses to object vs. internal motion. The exact mechanisms of how perception and pursuit process diverse motion signals remain unclear. For example, it remains unclear whether individual differences in patterns of perceptual bias are related to different interpretations of internal motion, or stimulus properties such as motion energy. Different manipu-

lations of stimuli and tasks are required to confirm these speculations. One manipulation could be the use of more realistic stimuli without ambiguity in the relationship between different motion signals, e.g., a flying and rotating volley ball (Fig. 3.1b). If ambiguity mediates the integration of internal and object motion, we would expect smaller diversity in perception with stimuli that have little ambiguity in how object and internal motion are related. Another manipulation could be to direct observers' attention to different parts of a stimulus, such as by emphasizing the importance of object or internal motion in separate versions of the task. Additional task instruction on the relevance of different motion signals might decrease the variability in perceptual responses. Moreover, stimulus parameters could be manipulated to present conditions with different net motion energies. If the ambiguity in direction signals indicated by motion energy contributes to the individual differences in perception, we should observe similar patterns of the perceptual bias with stimuli with strong net motion energy in the target direction. It would also be interesting to see whether pursuit bias is affected by these manipulations. If so, it would imply that perception and pursuit are affected by similar top-down modulations.

To examine whether the across-observer correlation between perception and pursuit is caused by shared motion processing or by a top-down perceptual modulation on pursuit, examination of the temporal dynamics in the relationship between perception and pursuit is needed. One limitation of the current study is that perception was only measured at the end of the trial, whereas eye movements were recorded continuously throughout the trial. As a result, observers could have had more processing time for the perceptual response than for the pursuit response. This difference in the available processing time between perceptual and pursuit measurements could contribute to their dissociation, even though perception and pursuit share processing of motion signals (Cardoso-Leite and Gorea, 2010). Probing perception at different time points and comparing it to pursuit at corresponding time points could further our understanding of the relationship between perception and pursuit over time. If motion processing is shared between perception and pursuit, we would expect perception to have similar temporal dynamics as pursuit (i.e., change of bias over time). In addition, we would expect a correlation between perception and pursuit biases with short display duration. If a correlation between perception and pursuit biases only exists when the display duration is long, it might be driven by a top-down perceptual modulation on pursuit rather than by shared low-level motion processing between perception and pursuit.

## **Conclusion**

Using RDKs with translating object motion and additional internal dot motion, we showed that smooth pursuit to object motion is biased in the direction of internal motion, whereas perception was unbiased on average, with striking individual differences between observers. Different functional demands of the two systems might have resulted in the dissociation between perception and pursuit when processing motion signals at different spatial scales. The overall lack of bias in perception and the potential contrast bias in perception found in more than half of the observers are consistent with the need of perception to perform object segregation from the scene. Pursuit performs signal integration and follows the average motion signal to maximize visual information collection within the scene.

## Chapter 4

# Expectations about motion direction affect perception and anticipatory smooth pursuit differently

Findings from the previous study suggest that when faced with diverse motion signals across different spatial scales, perception and pursuit are still correlated, even though having different final outcomes. In this study<sup>3</sup>, we further examine when processing signals across time, whether perception and anticipatory pursuit utilize past experience in the same way, and how they may interact.

### 4.1 Introduction

How we perceive and interact with the visual world depends not only on current visual input, but also on our experience with past sensory events. In Bayesian inference, this experience informs a prior—one's expectation of the probability of an event before any sensory evidence is present (de Lange et al., 2018; Seriès and Seitz, 2013). This study investigates how visual motion priors, based on long-term experience, affect visual perception and movement, and whether these two outcomes are controlled in the same way or differently by expectation. We use smooth pursuit eye movements—the eyes' continuous response to moving objects—as a model system for visually-guided movement to investigate this question. Smooth pursuit eye movements are closely related to the perception of visual motion (Gegenfurtner, 2016; Schütz et al., 2011; Spering and Montagnini, 2011). They rely on the integration of current motion information

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<sup>3</sup>A version of this study has been published as Wu, X., Rothwell, A. C., Spering, M., and Montagnini, A. (2021). Expectations about motion direction affect perception and anticipatory smooth pursuit differently. *Journal of Neurophysiology*, 125, 977–991. Contents are almost identical except for: 1. Editorial changes (e.g., changing "visually guided pursuit" to "visually-guided pursuit") to keep a consistent formatting throughout the dissertation; 2. Additional information/clarification in Methods: (a) Spatiotemporal parameters ( $\Delta x$  and  $\Delta t$ ) of the RDK stimuli (in "Visual stimuli and setup"), (b) Exact directions in context trials (in "Procedure and design"), (c) Explanation about coherence and anticipatory pursuit in the caption of Fig. 4.2, and (d) Clarification about the variables and factors in rmANOVA (in "Hypotheses and statistical analysis"); 3. Additional discussion of motion aftereffect and explanation of anti-Bayesian effects in Discussion ("Limitations and future directions").

with priors based on experience across just a few trials or across a longer-term context (Darlington et al., 2017; Deravet et al., 2018; Yang et al., 2012). Moreover, smooth pursuit can be triggered by the expectation of a certain motion direction even before the object's motion onset, a phenomenon known as anticipatory smooth pursuit (Kowler et al., 1984, 2019).

Previous research has revealed highly consistent effects of expectation on pursuit, but contrasting effects on motion perception. For example, anticipatory pursuit can be triggered when observers repeatedly view stimuli moving into the same direction (Kowler, 1989; Kowler et al., 2019). The eyes are then attracted to the expected motion direction before the onset of the stimulus (attraction bias in direction). These responses are not purely habitual but finely tuned to the strength of expectation (Damasse et al., 2018; Jarrett and Barnes, 2002; Santos and Kowler, 2017). Congruently, anticipatory pursuit velocity is proportional to the average velocity of the target across previous trials (attraction bias in speed) and strongly affected by events in the previous two trials (Maus et al., 2015). Furthermore, Bayesian integration models have been used to describe how priors would lead to attraction effects in visually-guided pursuit when combined with noisy visual motion signals (Behling and Lisberger, 2020; Bogadhi et al., 2013; Darlington et al., 2017; de Xivry et al., 2013; Deravet et al., 2018).

By contrast, perceptual studies have found evidence for both an attraction bias as well as for responses to be repelled away from the expected direction (repulsion bias; Jazayeri and Movshon 2007). In studies reporting attraction biases, estimates of direction, velocity, or orientation in a current trial are affected by events in previous trials such that an observer's perception would be biased in line with the motion information observed in previous trials. Such biases can build up quickly, within a few trials (Alais et al., 2017; Cicchini et al., 2018) or can be based on implicitly learning the statistical properties of a stimulus environment over many trials (Chalk et al., 2010; Kok et al., 2013; Seriès and Seitz, 2013), as described by Bayesian integration models. Perceptual repulsion biases have been observed across different visual tasks and features. In a speed estimation task in which observers had to judge whether the speed in the current trial was faster or slower than the average speed across all previous trials, observers tended to overestimate a current target's velocity when the average velocity across previous trials was slow and vice versa for fast velocity (Maus et al., 2015). Similar repulsion biases have been found in studies in which observers had to adjust the orientation of a test stimulus relative to an inducer stimulus, when both stimulus orientations differed by more than  $60^\circ$  between the previous and current trial (Fritsche et al., 2020). In this scenario, observers' adjustment responses were sometimes repelled away from the previous trial's stimulus orientation. In sum, expectation built across different timescales can result in a perceptual bias either in the same direction as the cue, prompt, or adaptor (attraction bias), or in the opposite direction (repulsion bias).

The current study directly compared effects of direction expectation on perception and anticipatory pursuit within the same trials to investigate whether both types of responses are affected similarly or differently, and how they interact. On one hand, attraction biases are commonly found in pursuit and in most perceptual studies that did not use adjustment tasks or reference comparisons. On the other hand, one study that directly compared velocity expectation effects reported opposite biases in speed discrimination and antic-

ipatory pursuit (Maus et al., 2015). Overall, it remains unclear whether motion priors affect perception and pursuit similarly or differently. We introduced different probabilities of motion direction in the current study, leading to an implicit expectation bias for future motion direction based on previous trial history. This manipulation allows us to investigate the effect of a general motion prior on perception and pursuit. In the following, we refer to effects of expectation as the behaviour triggered by manipulations of this statistical bias.

## 4.2 Methods

All three experiments were similar in terms of procedure and analyses. Experiment 1 was the main experiment, and the purpose was to compare the effect of expectation on motion direction discrimination and anticipatory pursuit. Control experiments 2 and 3 investigated alternative explanations for findings obtained in Experiment 1, testing interactions between anticipatory pursuit and perception, and effects of stimulus features, respectively. General methods are described for Experiment 1. Deviations in stimuli and procedures for control experiments are briefly described in Results.

### Observers

We recruited 10 observers (age mean = 26.20,  $SD = 5.41$  years; six females) with normal or corrected-to-normal visual acuity (at least 20/20 as assessed using an Early Treatment Diabetic Retinopathy Study chart) and no history of ophthalmologic, neurologic, or psychiatric disease. All observers participated in Experiment 1, eight of these observers (age mean = 27.38,  $SD = 5.40$  years; four females) also participated in Experiment 2, and nine (age mean = 26.56,  $SD = 5.61$  years; six females) also participated in Experiment 3. The sample size is comparable with previous studies ( $n = 9$  in Maus et al. 2015,  $n = 8$  in Santos et al. 2012,  $n = 6$  in Santos and Kowler 2017). The University of British Columbia Behavioural Research Ethics Board approved all experimental procedures, and all observers participated after giving written informed consent. Observers received \$35 CAD remuneration for participation per experiment.

### Visual stimuli and setup

Stimuli were random dot kinematograms (RDKs) presented in a static aperture of  $20^\circ$  diameter centred in the middle of the screen. Each RDK consisted of  $\sim 470$  (density  $1.5 \text{ dot/deg}^2$ ) uniformly distributed white dots ( $98 \text{ cd/m}^2$ ) on a grey background ( $22 \text{ cd/m}^2$ ). Each dot (diameter  $0.14^\circ$ ) moved at a constant speed of  $10^\circ/\text{s}$ . The duration of each frame ( $\Delta t$ ) is about 12 ms, at the rate equal to the screen refresh rate of 85Hz. the spatial displacement ( $\Delta x$ ) per frame is about 7 arcmin (4 pixels). The dots were labelled as signal or noise dots. Labels were updated and randomly reassigned every four frames ( $\sim 47$  ms). Signal dots always moved in the global motion direction of the RDK (left or right), whereas each noise dot moved in a random direction other than the signal direction with unlimited lifetime. When a dot moved out of the aperture, it reentered from the opposite side of the aperture. The coherence of the RDK was defined as the proportion of signal dots (0–100%).

Observers were seated in a dimly-lit room and viewed all stimuli on a  $\gamma$ -corrected  $39 \text{ cm} \times 29 \text{ cm}$  CRT

monitor (ViewSonic G255f; resolution  $1280 \times 1024$  pixels; refresh rate 85Hz). The viewing distance was 55 cm. Each observer's head was stabilized using a chin-and-forehead-rest. Stimuli and procedure were programmed in MATLAB R2018b (The MathWorks Inc., Natick, MA) and Psychtoolbox version 3.0.12 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

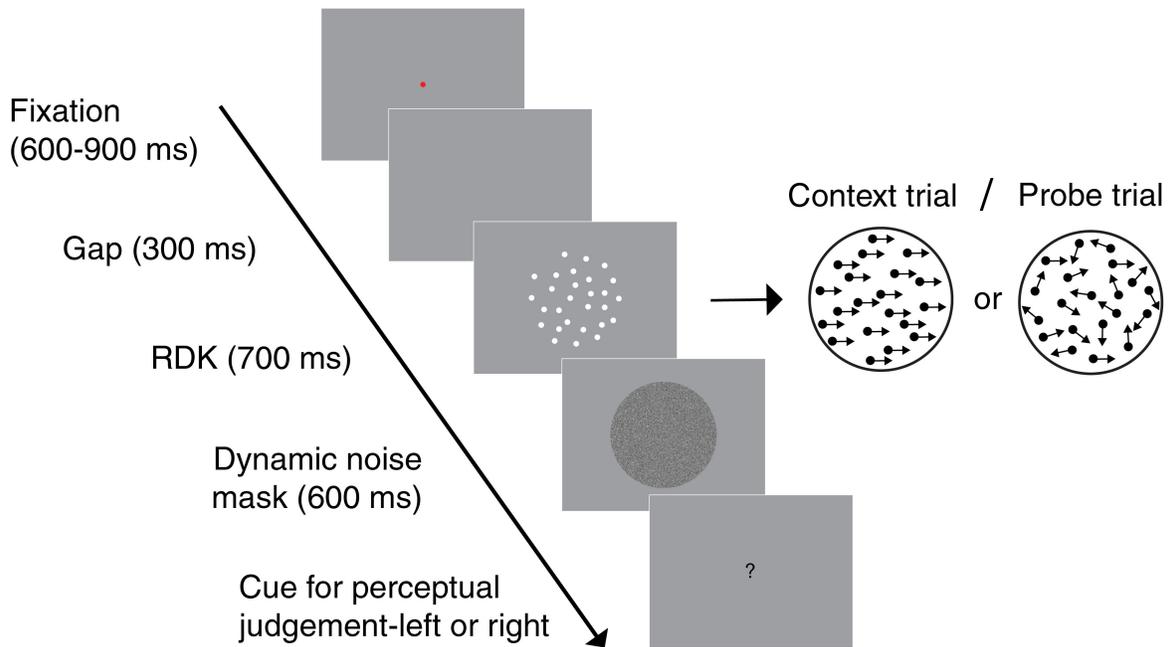
### **Procedure and design**

Figure 4.1 shows the trial timeline in Experiment 1. Observers were asked to fixate the centre of the screen when the red fixation point was on for 600–900 ms. Fixation was monitored online: if eye position was further than  $2^\circ$  from the centre of the fixation point, the fixation point turned white and the countdown of fixation duration was paused until the observer regained accurate fixation. A blank screen (gap; 300 ms) was shown to help induce anticipatory pursuit (Krauzlis and Miles, 1996). Observers were then asked to smoothly follow the global motion of the RDK (700 ms) with their eyes. A dynamic white-noise mask with luminance noise randomly assigned pixel by pixel (luminance range within  $7 \text{ cd/m}^2$  to  $46 \text{ cd/m}^2$ ) was shown after RDK offset for 600 ms to avoid potential carry-over effects from one trial to the next (Apthorp et al., 2011; Schwiedrzik et al., 2014). At the end of each trial, they were asked to report whether it moved left or right using the “left” or “right” arrow keys on the computer keyboard.

In each block, two types of trials were shown: 500 context trials containing nonambiguous motion direction (100% coherence) were randomly interleaved with 182 probe trials containing ambiguous motion (0, 5, 10, or 15% coherence). The purpose of the context trials was to build up an expectation of motion direction in a given block. RDKs in context trials moved either leftward or rightward. In each of three blocks of trials, presented in random order, we introduced different probabilities of motion direction in context trials, either 50%, 70%, and 90% probability of rightward or leftward motion. Blocks with higher probability of rightward and leftward motion were presented in different sessions; half of our sample of observers ( $n = 5$ ) saw only higher probabilities of rightward motion, and the other half saw only higher probabilities of leftward motion. The experiment was split up that way to reduce workload for each observer, because each block of trials took 60 min to complete for a total of 3h per observer. The first 50 trials in each block were always context trials. The purpose of the probe trials was to measure the effect of expectation on perception of motion direction, which would be prominent when visual input provided little evidence. To fairly compare perception and oculomotor anticipation, we also analyzed anticipatory pursuit in probe trials only. For all observers, probe trials consisted of equal numbers of leftward/rightward trials.

### **Eye movement recording and analysis**

In all three experiments, the position of the right eye was recorded using a video-based eye tracker at a sampling rate of 1,000 Hz (EyeLink 1000 desk-mounted, SR Research Ltd., Kanata, ON, Canada). Eye movements were then analyzed offline using custom-made MATLAB functions. Eye position, velocity, and acceleration data were filtered with a second-order Butterworth filter (cutoff frequencies of 15 Hz for position and 30 Hz for velocity and acceleration). Saccades were detected based on an acceleration criterion: the acceleration trace was segmented by zero-crossing points, and peak acceleration within each segment



**Figure 4.1:** Trial timeline in Experiment 1. A fixation point was shown for 600–900 ms, followed by a blank screen for 300 ms, and the RDK for 700 ms. A dynamic white-noise mask was presented after the RDK for 600 ms. A question mark is presented at the centre of the screen after the dynamic white-noise mask, indicating that participants could now report the perceived global motion direction. Two types of trials were presented: context trials with highest-coherence RDKs, and probe trials with low-coherence RDKs. The stimuli’s relative size and contrast are increased for presentation purposes. RDK, random-dot kinematograms.

was calculated. If at least two consecutive segments had absolute peak acceleration larger than  $400^\circ/s^2$ , these segments were defined as saccades. An acceleration threshold was used to accurately detect saccades of small amplitude and velocity during the anticipatory pursuit phase. Saccade detection was confirmed by visual inspection of the velocity traces in each trial. Saccades were then excluded from the analysis of smooth pursuit. Following previous studies (Maus et al., 2015; Santos and Kowler, 2017; Watamaniuk et al., 2017), anticipatory pursuit velocity was defined as the average horizontal eye velocity during the time window from 50 ms before to 50 ms after RDK onset. We also analyzed eye velocity gain (eye velocity relative to target velocity) during visually-guided pursuit, calculated during the time window from 300 to 600 ms after target onset. Trials with blinks during RDK presentation were manually labelled as invalid and excluded (1% across observers in Experiment 1, 0.5% in Experiment 2, and 0.7% in Experiment 3). Leftward direction is negative by convention.

### Perceptual response analyses

We did not observe systematic differences between the effects of rightward and leftward motion probability on the magnitude of anticipatory pursuit [Experiment 1:  $t(4) = 0.76$ ,  $p = 0.49$ , Cohen’s  $d = 0.94$ ] or percep-

tual bias [Experiment 1:  $t(4) = 1.07$ ,  $p = 0.34$ , Cohen’s  $d = 0.83$ ] and therefore merged data for different motion directions, presenting data as if higher probabilities of rightward motion were presented. Under each probability condition for each observer, we fitted a psychometric curve using the logistic function as shown below:

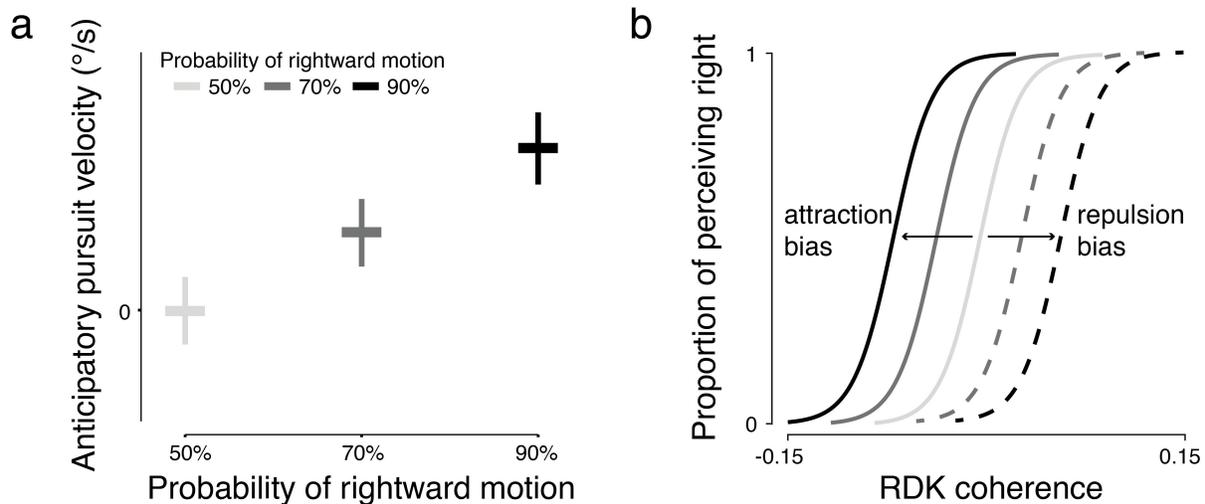
$$P(\text{perceiving right}) = (1 - \lambda) \frac{1}{1 + \exp -\beta(x - \alpha)} \quad (4.1)$$

Specifically,  $x$  is the signed motion coherence of RDK (negative for leftward motion),  $\alpha$  is the point of subjective equality (PSE) where observers reported both motion directions equally often (50% of the time),  $\beta$  is the slope representing the sensitivity of perception, and  $\lambda$  is the lapse rate (restricted to below 0.1 when fitting). In this study, a shift of the PSE across probability conditions would indicate a perceptual bias. A shift to the left indicates a perceptual attraction bias (i.e., with direction judgments being attracted toward the direction expectation of rightwards), and a shift to the right indicates a repulsion bias. A change in slope across probability conditions would indicate a change in sensitivity of perceptual judgments, where a steeper slope corresponds to higher sensitivity. Curve fitting was performed using the Palamedes toolbox version 1.9.0 in MATLAB (Prins and Kingdom, 2018).

### Hypotheses and statistical analysis

In Experiment 1, we aimed to test the following hypotheses. First, anticipatory pursuit is affected by direction expectation: the velocity of anticipatory pursuit scales positively with the target’s direction probability (attraction bias); a higher probability of rightward motion will lead to a higher velocity in anticipatory pursuit (Fig. 4.2a). Second, direction perception is affected by direction expectation: observers preferentially perceive the expected motion direction (attraction bias; Fig. 4.2b). Alternatively, perception could be biased away from the expected direction (repulsion bias; Fig. 4.2b), as has sometimes been reported in the literature. We further examined if expectation affected slope to investigate whether different prior probabilities might result in differences in sensitivity. To examine the expected effects of probability on anticipatory pursuit velocity, the magnitude of perceptual bias (shift of the PSE), and the sensitivity of perception (slope), we used one-way repeated-measures analyses of variance (ANOVA). Anticipatory pursuit velocity, PSE, or slope is the dependent variable, and *probability* (50%, 70%, or 90%) of motion direction in context trials is the within-subjects factor. In addition, to examine whether anticipatory pursuit velocity and the strength of any potential perceptual bias were correlated across conditions and observers, we fitted a linear mixed-effects model of PSE with *probability* and *anticipatory pursuit velocity* as fixed effects, and individual intercept as the random effect [formula:  $\text{PSE} \sim \text{anticipatory pursuit velocity} + \text{probability} + (1 \mid \text{observer})$ ]. Finally, we also examined the potential link between visually-guided pursuit and perception, and effects of *probability* on the velocity gain of visually-guided pursuit. Experiments 2 and 3 investigated alternative explanations of findings obtained in Experiment 1. Their logic and underlying hypotheses are described in Results.

Across experiments, we report generalized eta-squared ( $\eta_g^2$ ) as the effect size in one-way ANOVAs, and



**Figure 4.2:** Hypotheses for (a) attraction bias in anticipatory pursuit velocity and (b) attraction or repulsion bias in perception. (a) Anticipatory pursuit velocity increases with increasing probability of rightward motion in each block, reflecting an attraction bias. Note that anticipatory pursuit is not affected by the visual motion of the current trial. (b) The perceptual bias is reflected by a shift of the PSE at higher probabilities (70% and 90%) when compared with the 50% probability condition; a leftward shift (solid lines) indicates an attraction bias, a rightward shift (dashed lines) indicates repulsion bias. Negative value of RDK coherence indicates that the global motion direction is left. PSE, point of subjective equality; RDK, random-dot kinematograms.

partial eta-squared ( $\eta_p^2$ ) in two-way ANOVAs. For all experiments, we also report mean and 95% confidence interval (CI) of anticipatory pursuit velocity and PSE from 1,000 bootstrap simulations to supplement statistical hypothesis testing and provide quantitative estimates of the variability of sample estimates. To supplement tests yielding non-significant effects in our statistical analyses, we performed equivalence tests (Lakens et al., 2018). Specifically, two one-sided paired  $t$  tests were conducted to examine if the difference between two groups was within the smallest effect size of interest (the null hypothesis for these tests would be that there is a significantly large difference). We set the smallest effect size of interest to Cohen's  $d = 0.36$ , which is the effect size that a study with 20 observers can detect with 33% power and an  $\alpha$  of .05 in a two-sided paired  $t$  test. We report the  $t$  test with the smaller  $t$  value (thus larger  $p$  value). If the larger  $p$  value is smaller than .05, the hypothesis that there is a significant difference is rejected; otherwise, it would indicate insufficient evidence to conclude whether there is a difference. The statistical tests were conducted in R version 3.6.0 (package "TOSTER," Lakens 2017; package "lme4," Bates et al. 2015; package "ez," Lawrence 2016; R Core Team, R Core Team 2019) and MATLAB R2020a.

## 4.3 Results

### Experiment 1

### ***Evidence for attraction bias in anticipatory pursuit***

Across observers and trials, we found that the velocity of the anticipatory pursuit response scaled positively with the probability of a given motion direction. Figure 4.3a shows an example of individual eye velocity traces, and Figure 4.3b shows group-averaged eye velocity traces in probe trials, indicating that anticipatory pursuit velocity increases with increasing probability of rightward motion. These observations were confirmed by a significant main effect of *probability* on anticipatory pursuit velocity (Fig. 4.3c),  $F(2, 18) = 28.19$ ,  $p < 0.001$ ,  $\eta_g^2 = 0.19$ . As a complementary method to these statistics, the bootstrapped mean and 95% CI of anticipatory pursuit velocity confirmed our findings (50%:  $0.24 \pm 0.01^\circ/\text{s}$ ; 70%:  $0.70 \pm 0.01^\circ/\text{s}$ ; 90%:  $1.26 \pm 0.01^\circ/\text{s}$ ).

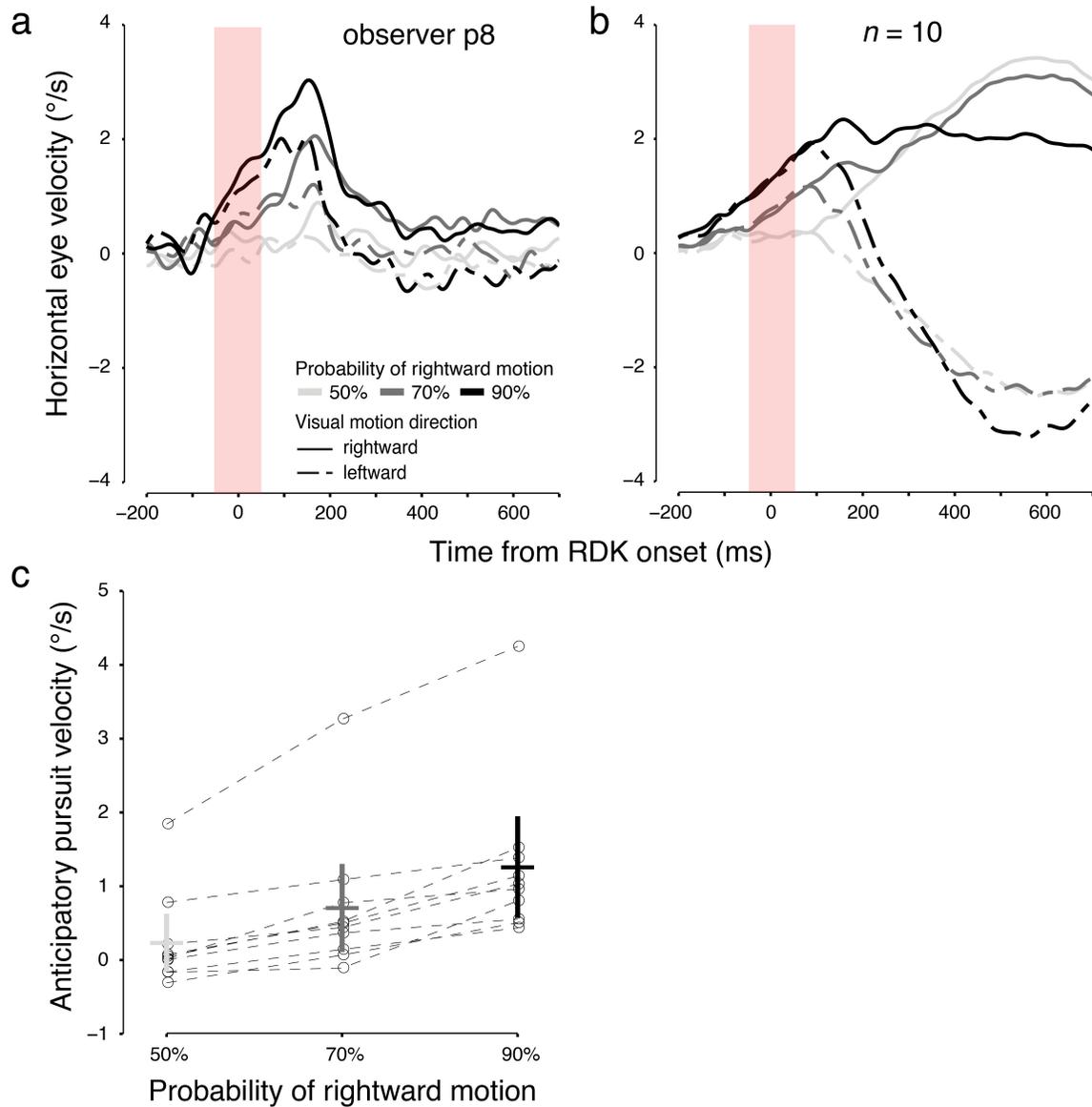
### ***Evidence for repulsion bias in direction perception***

Perceptual results are incongruent with what we observed for anticipatory pursuit. We found a systematic rightward shift in the PSE at the individual observer level (Fig. 4.4a) as well as across observers (Fig. 4.4b), indicating a perceptual bias away from the high-probability motion direction. When rightward trials had a higher probability in context trials, observers tended to perceive leftward direction more often in probe trials. These observations were confirmed by a significant main effect of *probability* on the PSE (Fig. 4.4b),  $F(2, 18) = 20.36$ ,  $p < 0.001$ ,  $\eta_g^2 = 0.34$ . The bootstrapped mean and 95% CI of the PSE confirmed these statistical results (50%:  $-0.02 \pm 0.002$ ; 70%:  $0.0003 \pm 0.002$ ; 90%:  $0.04 \pm 0.0002$ ). We did not observe any significant effects of *probability* on slope [ $F(2, 18) = 0.78$ ,  $p = 0.48$ ,  $\eta_g^2 = 0.02$ ], indicating that sensitivity did not change across probability conditions. The bootstrapped mean and 95% CI of slope were  $31.31 \pm 5.26$  for 50%,  $31.72 \pm 2.14$  for 70%, and  $29.87 \pm 3.93$  for 90%.

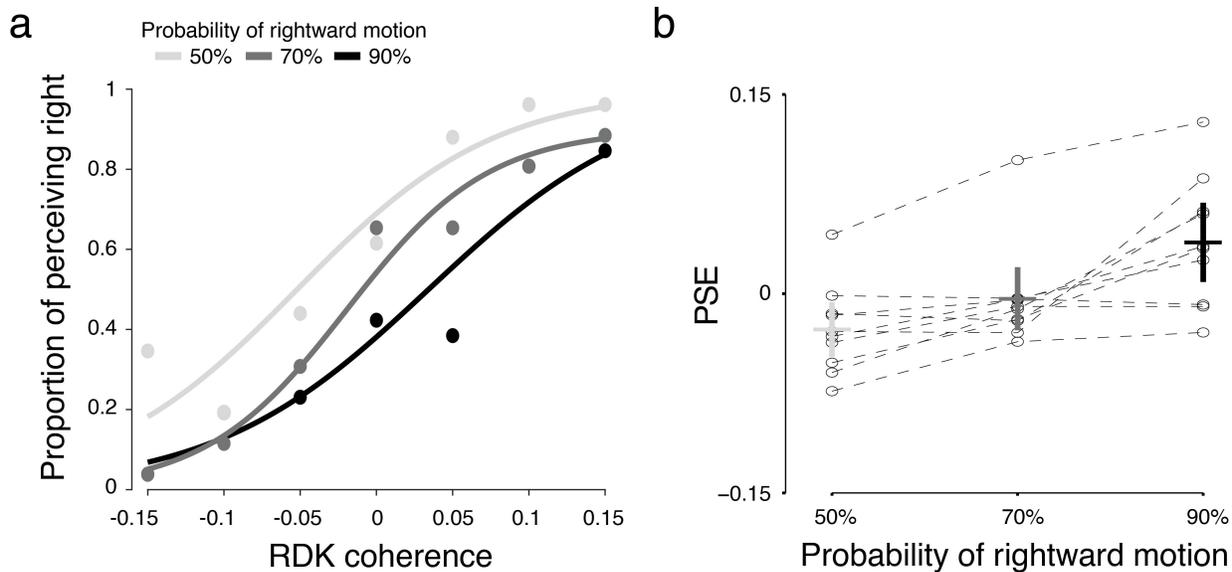
We did not find any dependencies between PSE and anticipatory pursuit velocity in addition to the fact that they both changed with probability. The fixed effect of anticipatory pursuit velocity in the linear mixed-effects model of PSE [PSE  $\sim$  anticipatory pursuit velocity + probability + (1 | observer)] was not significant [estimate  $\pm$  SD =  $-0.0002 \pm 0.01$ ,  $t(20.31) = -0.16$ ,  $p = 0.87$ ], and only the fixed effect of probability was significant [estimate  $\pm$  SD =  $0.002 \pm 0.0004$ ,  $t(30.00) = 4.60$ ,  $p < 0.001$ ]. To illustrate this, we show the across-observer relationship between probability-induced changes of anticipatory pursuit velocity and probability-induced changes of PSE (Fig. 4.5). The probability-induced changes were calculated as the fitted slopes of anticipatory pursuit velocity (as shown in Fig. 4.3c) or PSE (as shown in Fig. 4.4b) across probability conditions. Consistent with the non-significant main effect of anticipatory pursuit velocity on PSE in the linear mixed-effects model, there is no clear pattern of proportionality and for instance observers with larger changes in anticipatory pursuit velocity do not necessarily show larger changes in PSE.

Taken together, our results point to a differential effect of motion direction probability on anticipatory pursuit, reflecting an attraction bias, and direction perception, reflecting a repulsion bias. To explore this further, we next examined the potential link between visually-guided pursuit and perception and analyzed the effect of probability on visually-guided pursuit velocity gain.

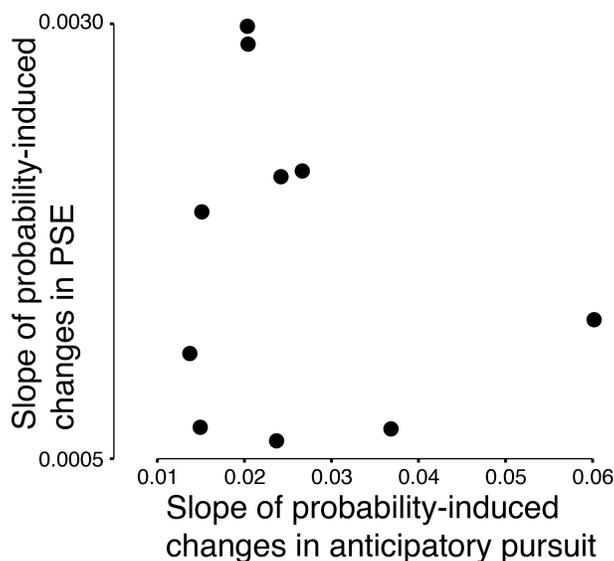
### ***Visually-guided pursuit is aligned with direction perception***



**Figure 4.3:** (a) Example trial-average horizontal eye velocity traces in probe trials (leftward or rightward motion direction as indicated by line type) for different probability conditions (indicated by line colour) for one representative observer in Experiment 1. The red shaded area indicates the analysis window for anticipatory pursuit. This particular observer had little visually-guided pursuit in probe trials. (b) Group-average horizontal eye velocity traces in probe trials for different probability conditions in Experiment 1 for  $n = 10$ . Line types in A and B denote motion direction and probability of rightward motion. (c) Horizontal anticipatory pursuit velocity in Experiment 1 averaged across the time interval indicated as shaded area in (a). Horizontal bars indicate the mean anticipatory pursuit velocity across observers, and vertical bars indicate the 95% CI. The circles indicate the mean anticipatory pursuit velocity of individual observers, connected by dashed lines across probability conditions. Results were the same even if excluding the one outlier who had relatively high anticipatory pursuit velocity. CI, confidence interval; RDK, random-dot kinematograms.



**Figure 4.4:** (a) Example psychometric curves from the same individual observer shown in Fig. 4.3a. Negative coherence represents leftward direction. (b) PSE in Experiment 1 ( $n = 10$ ). PSE, point of subjective equality; RDK, random-dot kinematograms.



**Figure 4.5:** Relationship between probability-induced changes in anticipatory pursuit velocity and PSE across observers in Experiment 1. Each dot represents the data of one observer. PSE, point of subjective equality.

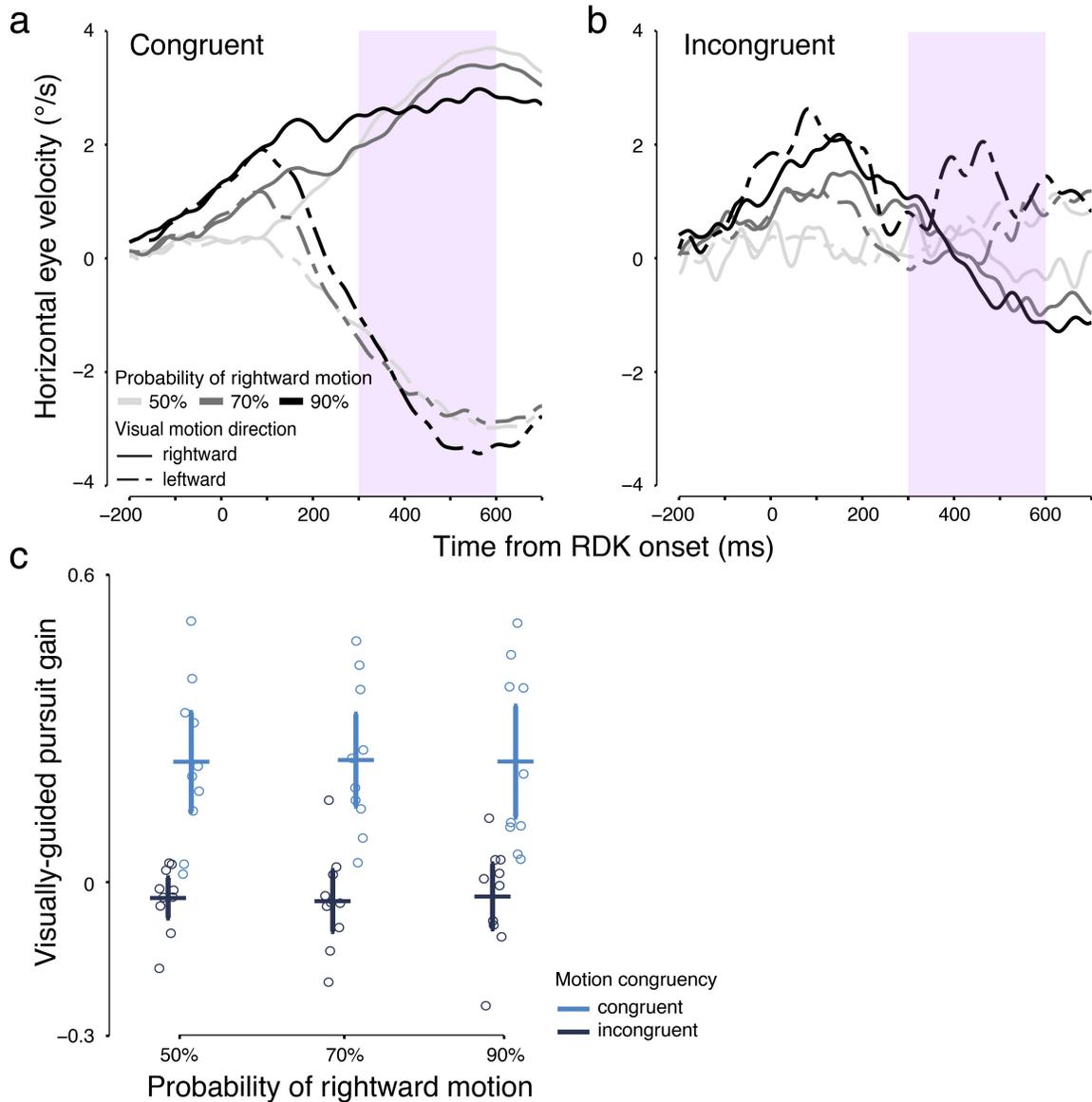
Whereas anticipatory pursuit is mostly driven by expectation, visually-guided pursuit is tuned to the visual properties of the target and is known to strongly covary with motion perception (Spering and Montagnini, 2011). Previous research has demonstrated that smooth pursuit can be elicited by perceived illusory motion

rather than by physical motion (Madelain and Krauzlis, 2003; Montagnini et al., 2006). Therefore, visually-guided pursuit could follow different result patterns from anticipatory pursuit and be more aligned with perception.

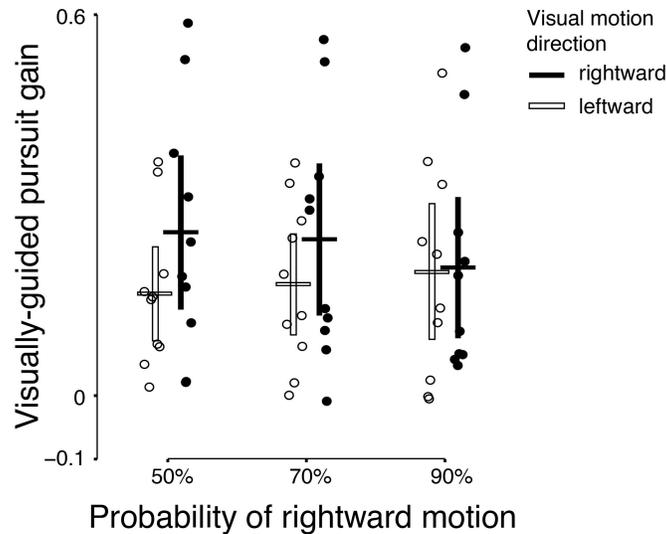
Here, we investigated whether visually-guided pursuit was more in line with an attraction bias (as in anticipatory pursuit) or followed a repulsion bias (as in perception). We compared eye velocity gain in conditions in which the perceptual judgment corresponded to the physical motion direction (congruent) with conditions where perceptual judgments went in the opposite direction to the physical motion (incongruent). Figure 4.6 shows average velocity traces in probe trials across all observers for congruent (Fig. 4.6a) versus incongruent trials (Fig. 4.6b). Note that this categorization of congruency is agnostic on whether perception followed the expected motion direction or the opposite one and merely reflects how closely perception matched physical target motion. Whereas late visually-guided pursuit followed the visual motion direction in congruent trials (shaded areas in Fig. 4.6a), pursuit followed visual motion direction less in incongruent trials (Fig. 4.6b) with a tendency to be directed into the opposite (perceived) direction, resulting in smaller or negative gains. This is confirmed by a significant main effect of *congruency* on velocity gain [Fig. 4.6c;  $F(1,9) = 20.65$ ,  $p = 0.001$ ,  $\eta_p^2 = 0.70$ ]. The main effect of *probability* [ $F(2,18) = 0.049$ ,  $p = 0.953$ ,  $\eta_p^2 = 0.005$ ] or the *congruency*  $\times$  *probability* interaction [ $F(2,18) = 0.051$ ,  $p = 0.950$ ,  $\eta_p^2 = 0.006$ ] were not significant. This difference in visually-guided pursuit between congruent and incongruent conditions persisted across different levels of motion coherence (not shown). However, we noticed that there were inconsistencies across observers, and some observers tend to have little visually-guided pursuit in probe trials in general (such as the example observer in Fig. 4.3a), or in incongruent trials (Fig. 4.6c, gain around zero). Therefore, although visually-guided pursuit was biased toward the opposite direction than visual motion (i.e., the perceived direction) in incongruent trials, it did not always strictly move in the perceived direction.

Further, we examined if expectation had an effect on visually-guided pursuit, by analyzing the effect of *probability* on visually-guided pursuit gain. Late-phase visually-guided pursuit in rightward probe trials seemed to have lower velocity in blocks with higher probability of rightward motion (see Fig. 4.3b, can also be seen in Fig. 4.6a with the majority of probe trials). Since direction expectation might affect visually-guided smooth pursuit differently for rightward and leftward motion trials, we included *visual motion direction* as a second factor in the two-way ANOVA on visually-guided pursuit gain. If the observed decrease in eye velocity with increased probability across blocks was true, a significant main effect of *probability* and possibly a significant interaction effect of *probability*  $\times$  *visual motion direction* could be observed. However, the interaction effect [ $F(2,18) = 1.54$ ,  $p = 0.24$ ,  $\eta_p^2 = 0.15$ ; Fig. 4.7], the main effect of *probability* [ $F(2,18) = 0.58$ ,  $p = 0.57$ ,  $\eta_p^2 = 0.06$ ], or the main effect of *visual motion direction* [ $F(1,9) = 1.87$ ,  $p = 0.20$ ,  $\eta_p^2 = 0.17$ ] were non-significant. This could be due to the large individual variability—some observers had little visually-guided pursuit in probe trials across probability conditions (gain close to zero), likely due to the low RDK coherence.

Notwithstanding a lack of evidence for expectation effects on visually-guided pursuit, this part of the



**Figure 4.6:** (a) Group-averaged ( $n = 10$ ) horizontal eye velocity traces in probe trials in which visual motion directions were congruent (3967 trials total) with perceived directions across different probability conditions in Experiment 1. The purple shaded area indicates the analysis window for late-phase pursuit; an early cutoff was applied to reduce the effect of anticipatory deceleration before the end of each trial (at 700 ms). (b) Group-averaged ( $n = 10$ ) horizontal eye velocity traces in probe trials in which visual motion directions were incongruent (649 trials total) with perceived directions across different probability conditions in Experiment 1. (c) Late-phase visually-guided pursuit gain in probe trials grouped by motion congruency across different probability conditions in Experiment 1 ( $n = 10$ ). Higher gain indicates that the eyes follow the visual motion better, and negative gain indicates that the eyes are moving in the opposite direction to the visual motion direction. Horizontal bars indicate the mean visually-guided pursuit gain across observers, and vertical bars indicate the 95% CI. The circles indicate the mean visually-guided pursuit gain of individual observers. CI, confidence interval; RDK, random-dot kinematograms.



**Figure 4.7:** Late-phase visually-guided pursuit gain in probe trials grouped by visual motion direction across different probability conditions in experiment 1 ( $n = 10$ ). Circles indicate the mean visually-guided pursuit gain of individual observers.

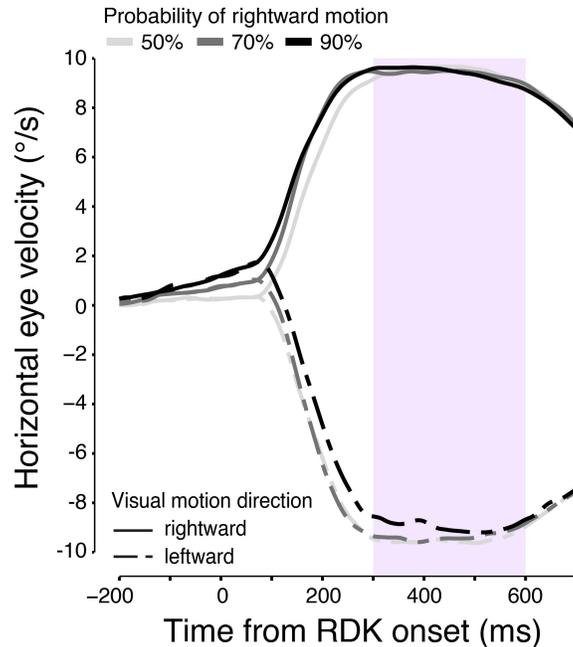
pursuit response was more aligned with perception than anticipatory pursuit. This finding indicates that late-phase pursuit is driven by signals that are more coherent with those signals driving perceptual judgments than those driving anticipatory pursuit.

#### *No motor adaptation of visually-guided pursuit in context trials*

To confirm that any biases in anticipatory pursuit and perception were not due to motor adaptation in visually-guided smooth pursuit, we tested whether direction probability had an effect on visually-guided pursuit in context trials (Fig. 4.8). The first 50 context trials in each block were excluded from this analysis, because these trials might be used to build up an expectation of motion direction. A one-way ANOVA with *probability* as the factor yielded no significant main effect of *probability* on visually-guided pursuit gain [ $F(2, 18) = 0.51, p = 0.61, \eta_g^2 = 0.01$ ]. This indicates that motor adaptation is unlikely to affect perception and pursuit in probe trials.

### **Experiment 2**

To further explore the mechanisms underlying the dissociation between expectation effects on anticipatory pursuit and perception, we conducted two control experiments. One potential problem with our paradigm might be that anticipatory pursuit during the earliest phase of the presentation of the low-coherence RDK elicits retinal image motion in the opposite direction than the expected one. This motion signal could have informed the perceptual choice, explaining the repulsion bias. In Experiment 2, we therefore tested whether the observed perceptual bias was affected by this negative retinal motion signal by manipulating anticipatory pursuit magnitude. To reduce anticipatory pursuit, we showed the fixation point until RDK onset, omitting



**Figure 4.8:** Group-averaged ( $n = 10$ ) horizontal eye velocity traces in context trials across different probability conditions in Experiment 1. The purple shaded area denotes the chosen analysis interval for visually-guided pursuit gain. RDK, random-dot kinematograms.

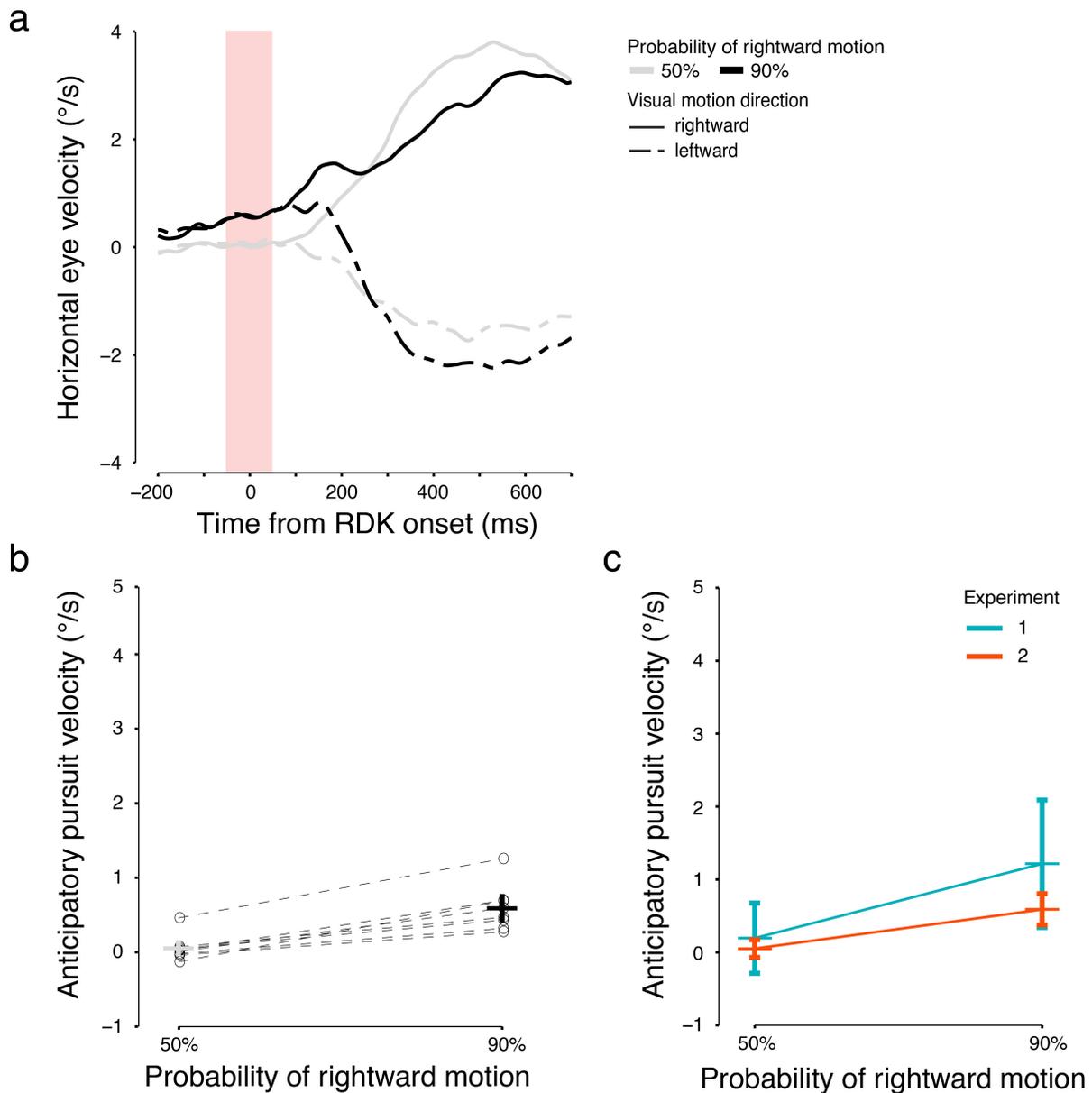
the 300-ms gap introduced in Experiment 1, and instructed observers to maintain fixation until the stimulus started moving. Each observer completed two blocks (50% and 90% probability of rightward motion). All other procedures were the same as in Experiment 1.

To confirm that anticipatory pursuit was reduced in Experiment 2 as compared with Experiment 1, we performed a two-way repeated measures ANOVA with *experiment* and *probability* as factors. An *experiment*  $\times$  *probability* interaction effect on anticipatory pursuit velocity would indicate a change in anticipatory pursuit magnitude from one experiment to the other. If anticipatory pursuit induced the perceptual bias, reduced anticipatory pursuit magnitude in Experiment 2 should result in a smaller perceptual bias. This interpretation would be supported by a significant *experiment*  $\times$  *probability* interaction effect on PSE.

#### ***Anticipatory pursuit was significantly reduced with prolonged fixation***

The experimental manipulation of prolonging fixation in Experiment 2 yielded the expected reduction in anticipatory pursuit velocity from  $1.26 \pm 1.11^\circ/\text{s}$  (mean  $\pm$  *SD*) in Experiment 1 to  $0.57 \pm 0.30^\circ/\text{s}$  in Experiment 2 at the highest probability of rightward motion (Fig. 4.9, a, b). This observation was confirmed by a significant *experiment*  $\times$  *probability* interaction [Fig. 4.9c;  $F(1, 7) = 7.20$ ,  $p = 0.03$ ,  $\eta_p^2 = 0.51$ ]. Despite lower overall velocity, higher probability of rightward motion continued to induce higher anticipatory pursuit velocity, reflected in a main effect of *probability* [ $F(1, 7) = 37.81$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.84$ ]. Congruently, the bootstrapped mean and 95% CI of anticipatory pursuit velocity in Experiment 2 were  $0.05 \pm 0.01^\circ/\text{s}$  for 50% and  $0.59 \pm 0.01^\circ/\text{s}$  for 90%. The main effect of *experiment* was not significant [ $F(1, 7) = 2.06$ ,

$p = 0.19, \eta_p^2 = 0.23$ ].



**Figure 4.9:** (a) The group-averaged ( $n = 8$ ) horizontal eye velocity traces in probe trials across different probability conditions in Experiment 2. (b) Horizontal anticipatory pursuit velocity in Experiment 2 ( $n = 8$ ). (c) The comparison of anticipatory pursuit velocity between Experiments 1 and 2. The horizontal bars show the mean across observers ( $n = 8$  for both experiments), and the error bars show the 95% CI. CI, confidence interval; RDK, random-dot kinematograms.

In addition, since perceptual performance is quantified by a probabilistic measure whereas anticipatory pursuit velocity is a continuous variable, we tested if the anticipatory pursuit was still reduced in Experi-

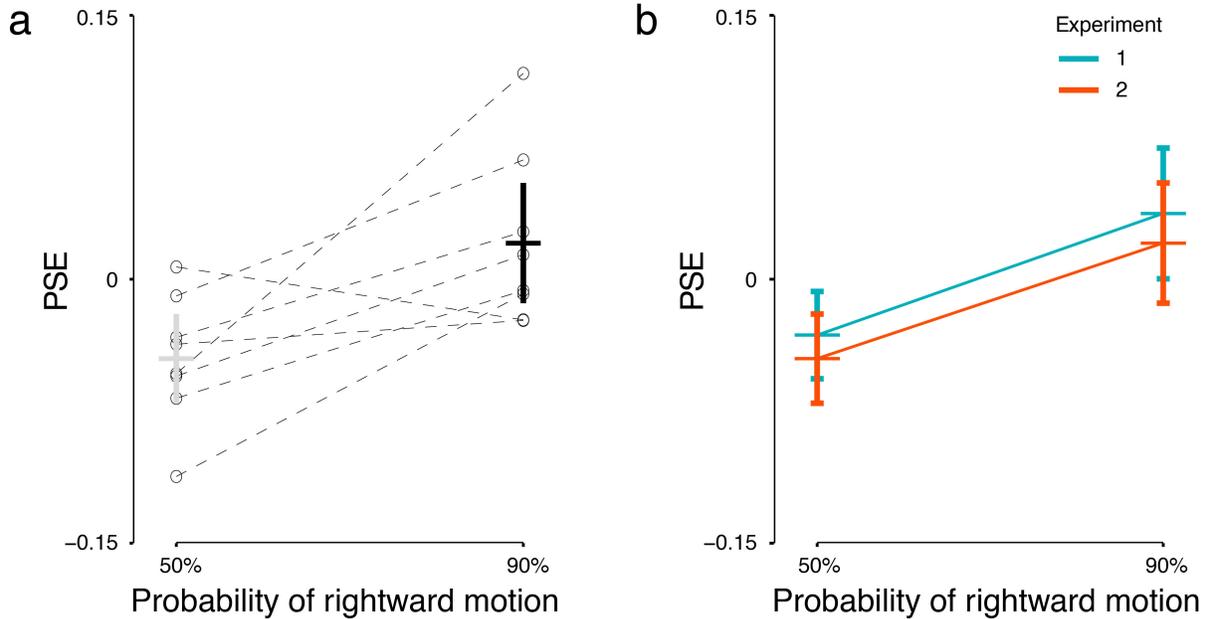
ment 2 with respect to Experiment 1 even when using a probabilistic measure. As by definition anticipatory pursuit is not affected by the motion coherence of the upcoming visual stimulus, and thus an “oculometric function” is not feasible, we simply binarized anticipatory pursuit into leftward and rightward, then calculated the proportion of trials with rightward anticipatory pursuit in each probability condition. Specifically, mean anticipatory pursuit velocity in the 50% block is used as the baseline, and anticipatory pursuit is classified as rightward if its velocity is larger than baseline. The proportion of trials with rightward anticipatory pursuit in the 90% block was significantly reduced from  $85.75 \pm 6.90\%$  in Experiment 1 to  $75.91 \pm 11.22\%$  in Experiment 2 [ $t(7) = 3.21$ ,  $p = 0.01$ , Cohen’s  $d = -1.14$ ], consistent with the reduction of mean anticipatory pursuit velocity.

### ***Persistent perceptual bias despite reduced anticipatory pursuit velocity***

Despite the successful reduction in anticipatory pursuit velocity, we did not observe a decreased repulsion bias (rightward shift of the PSE; Fig. 4.10a) in perceptual judgments in Experiment 2. This observation was confirmed by a significant main effect of *probability*,  $F(1, 7) = 22.91$ ,  $p = 0.002$ ,  $\eta_p^2 = 0.77$ , and a lack of *experiment*  $\times$  *probability* interaction [Fig. 4.10b;  $F(1, 7) = 0.001$ ,  $p = 0.97$ ,  $\eta_p^2 = 0.0002$ ]. The bootstrapped mean and 95% CI of the PSE were  $-0.04 \pm 0.003$  for 50% and  $0.02 \pm 0.002$  for 90%. The main effect of *experiment* was not significant [ $F(1, 7) = 4.54$ ,  $p = 0.07$ ,  $\eta_p^2 = 0.39$ ]. To further test if *experiment* has no effect on the perceptual bias, which can be calculated as the difference of PSE between the 90% and 50% blocks, we did equivalence tests of the difference of PSE across experiments. Both one-sided paired  $t$  tests showed non-significant results [ $t(7) = -0.86$ ,  $p = 0.21$  for the test with a larger  $p$  value], indicating insufficient evidence to support a null effect. Together, these results show that the negative retinal image motion induced by anticipatory pursuit is unlikely to cause the repulsion bias, but a firm conclusion of the null effect requires further confirmation.

### **Experiment 3**

In all experiments presented so far, we used a noise mask following RDK presentation (Fig. 4.1) to reduce potential motion aftereffects. Such aftereffects have been observed in perception (Mather et al., 2008) and pursuit (Braun et al., 2006). An alternative explanation for the perceptual repulsion effect observed in experiments 1 and 2 could be that prolonged exposure to a high-coherence moving stimulus in context trials produces a perceptual aftereffect (a form of low-level sensory adaptation) despite the mask. One way to reduce potential effects of motion aftereffects or other similar forms of sensory adaptation is to lower the motion signal strength of the adaptor, for example, by reducing its luminance contrast (Keck et al., 1976). It is well known that the response of neurons in motion-sensitive middle temporal cortex (area MT) is modulated by motion coherence (Händel et al., 2007). In Experiment 3, we therefore reduced the coherence of the RDK in context trials to investigate whether such a manipulation would weaken the perceptual repulsion bias. We reduced motion coherence of RDKs in context trials to 25 on average (coherence levels of 20% and 30% randomly assigned to half of the context trials in each block). This coherence level is considered to be above perceptual thresholds for direction discrimination in adults (Meier and Giaschi, 2014) and yielded



**Figure 4.10:** (a) PSE in probe trials across different probability conditions in Experiment 2 ( $n = 8$ ). (b) The comparison of PSE between Experiments 1 and 2 ( $n = 8$  in each experiment). Horizontal bars show the mean across observers, and the error bars show the 95% CI. CI, confidence interval; PSE, point of subjective equality.

judgments of  $>99\%$  correct accuracy in context trials in our experiment. We therefore expected that the perceived probability of context trials (50% and 90%) remained the same as in previous experiments. All other procedures were the same as in Experiment 1.

First, we assessed whether coherence impacted visually-guided pursuit in context trials to confirm that the coherence manipulation successfully reduced the motion signal. We conducted a two-way repeated-measures ANOVA on pursuit gain with *experiment* and *probability* as factors. A significant main effect of *experiment* would imply a reduction in motion signal due to the reduced coherence. To examine if motion coherence has an effect on anticipatory pursuit, we conducted a two-way repeated-measures ANOVA on anticipatory pursuit velocity with *experiment* and *probability* as factors. A significant interaction would indicate that anticipatory pursuit was modulated by motion signal strength in context trials. Second, to examine whether RDK coherence in context trials affects perception, we conducted a two-way repeated-measures ANOVA on PSE with *experiment* and *probability* as factors. If RDK coherence in context trials affected the repulsion bias, we should find a significant interaction.

#### ***Low-coherence context trials elicit weaker visually-guided and anticipatory smooth pursuit***

The experimental manipulation of motion coherence yielded the expected reduction in visually-guided pursuit gain in context trials (Experiment 1: mean =  $0.89 \pm 0.11$  across observers and probability conditions, Experiment 3: mean =  $0.49 \pm 0.16$ ). This observation was confirmed by a significant main effect of *exper-*

iment on pursuit gain [ $F(1, 8) = 192.62, p < 0.001, \eta_p^2 = 0.96$ ]. No significant main effect of *probability* [ $F(1, 8) = 1.66, p = 0.23, \eta_p^2 = 0.17$ ] or interaction [ $F(1, 8) = 1.68, p = 0.23, \eta_p^2 = 0.17$ ] was found. This confirmed that a reduction in motion coherence elicited a weaker motion signal and therefore lower pursuit gain in context trials.

Similarly, the experimental manipulation of motion coherence in context trials reduced anticipatory pursuit velocity at the highest probability of rightward motion in probe trials (Experiment 1: mean =  $1.26 \pm 1.11^\circ/\text{s}$ ; Experiment 3: mean =  $0.62 \pm 0.62^\circ/\text{s}$ , Fig. 4.11a, b). This observation was confirmed by a significant *experiment*  $\times$  *probability* interaction effect [ $F(1, 8) = 32.39, p < 0.001, \eta_p^2 = 0.80$ ], indicating that the effect of *probability* was smaller in Experiment 3 than in Experiment 1 (Fig. 4.11c). The main effect of *probability* was also significant [ $F(1, 8) = 23.29, p = 0.001, \eta_p^2 = 0.74$ ], and the main effect of *experiment* was not significant [ $F(1, 8) = 5.10, p = 0.05, \eta_p^2 = 0.39$ ]. The bootstrapped mean and 95%CI of anticipatory pursuit velocity in Experiment 3 were  $0.17 \pm 0.01^\circ/\text{s}$  for 50% and  $0.61 \pm 0.01^\circ/\text{s}$  for 90%. Consistently, the proportion of trials with rightward anticipatory pursuit in the 90% block, relative to the baseline anticipatory velocity in the 50% block, was significantly reduced in Experiment 3 [ $70.11 \pm 7.44\%$ ,  $t(8) = 4.88, p = 0.001$ , Cohen's  $d = -1.63$ ].

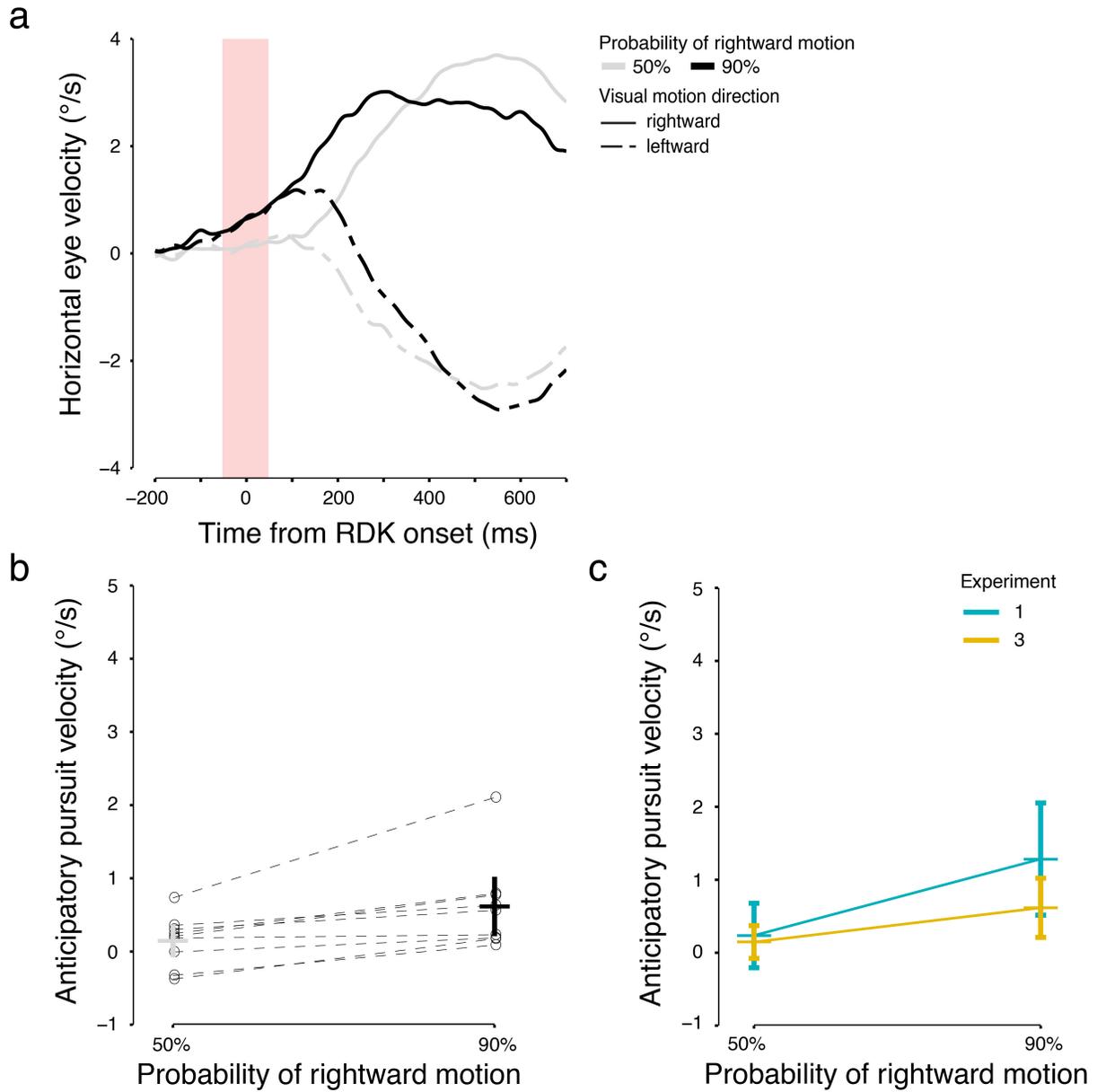
#### ***Persistent perceptual bias despite reduced motion coherence***

We found a reduction in visually-guided pursuit velocity, confirming that a lower-coherence stimulus shown in context trials elicited weaker pursuit, and thus was less likely to cause sensory adaptation. However, we did not find a significant difference in perceptual bias (Fig. 4.12). This observation was confirmed by a lack of *experiment*  $\times$  *probability* interaction on the PSE [ $F(1, 8) = 0.53, p = 0.49, \eta_p^2 = 0.06$ ], indicating a similar magnitude of perceptual bias in both experiments (Fig. 4.12b). The main effect of *probability* was significant [ $F(1, 8) = 44.97, p < 0.001, \eta_p^2 = 0.85$ ], and the main effect of *experiment* was not significant [ $F(1, 8) = 0.13, p = 0.73, \eta_p^2 = 0.02$ ]. Congruently, the bootstrapped mean and 95% CI of the PSE were  $-0.02 \pm 0.002$  for 50% and  $0.05 \pm 0.002$  for 90%. Yet, equivalence tests of the difference of PSE across experiments showed non-significant results [ $t(8) = 0.70, p = 0.25$ ], indicating insufficient evidence to clearly support a null effect.

In summary, results from Experiment 3 suggest that the perceptual bias was not purely an aftereffect induced by repeated exposure to strong motion signals, because reduced motion coherence in the context trial history did not modulate the perceptual repulsion bias.

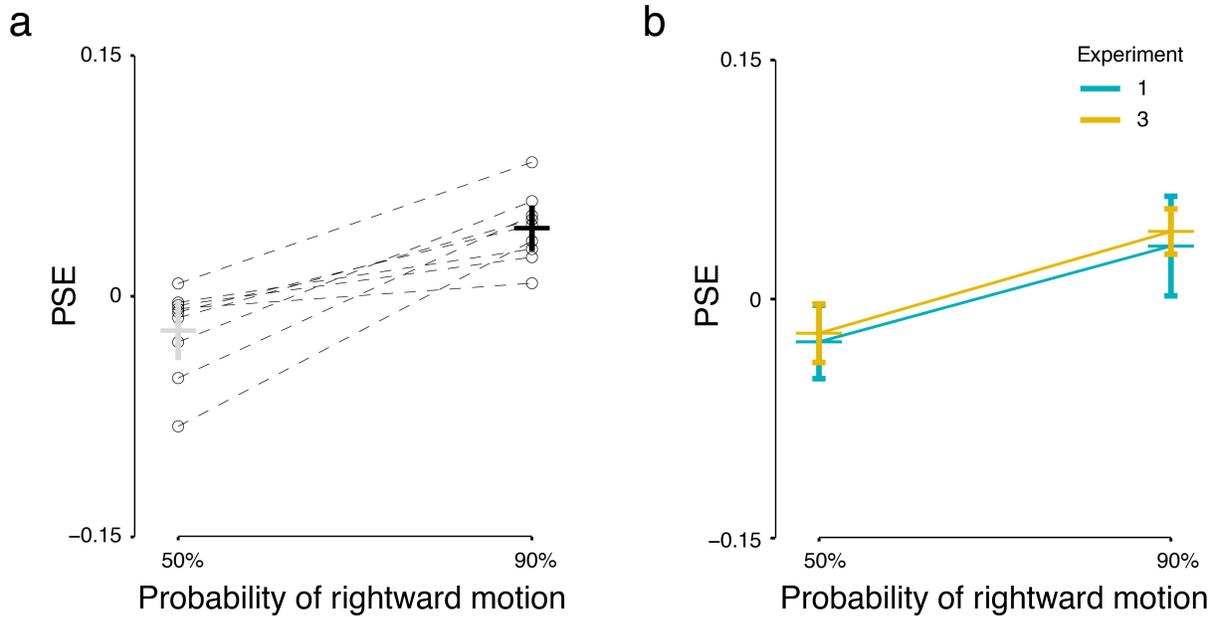
## **4.4 Discussion**

By introducing a prior based on different probabilities of rightward motion, we tested how expectation affected anticipatory pursuit and direction perception. Anticipatory pursuit was directed toward the highest probability direction in a given block of trials. By contrast, the direction of perceptual judgments was repelled away from the most probable direction. This repulsion bias was unlikely to be caused by anticipatory pursuit (Experiment 2) or sensory adaptation (Experiment 3). More generally, results from Experiment 2



**Figure 4.11:** (a) The averaged ( $n = 9$ ) horizontal eye velocity traces in probe trials across different probability conditions in Experiment 3. (b) Horizontal anticipatory pursuit velocity in Experiment 3 ( $n = 9$ ). (c) The comparison of anticipatory pursuit velocity between experiments 1 and 3 ( $n = 9$  in each experiment). Horizontal bars show the mean across observers, and the error bars show the 95% CI. CI, confidence interval; RDK, random-dot kinematograms.

together with a previous study showing that the opposite perceptual bias persisted even when observers fixated through the whole trial (Maus et al., 2015) suggest that eye movements are unlikely to be the cause of the opposite perceptual bias.



**Figure 4.12:** (a) PSE in probe trials across different probability conditions in Experiment 3 ( $n = 9$ ). (b) Comparison of PSE between experiments 1 and 3 ( $n = 9$  in each experiment). Horizontal bars show the mean across observers, and the error bars show the 95% CI. CI, confidence interval; PSE, point of subjective equality.

These results make a novel contribution to the literature on the comparison between perception and pursuit and highlight that motion perception does not necessarily rely on expectation in the same way as early, anticipatory pursuit responses do. These findings are generally congruent with a previous study investigating trial history effects in the velocity domain (Maus et al., 2015). In that study, the authors presented random sequences of brief, dot-motion stimuli with different speeds. Observers were asked to track the motion with their eyes and judge whether the current trial's speed was faster or slower than the speed averaged across previous trials. Whereas anticipatory pursuit scaled with previous target speed, perceptual judgments were faster after slow stimuli and vice versa for fast stimuli, indicating a similar repulsion effect as observed for motion direction in the current study. Taken together, our study and the previous study show that opposite effects on perception and anticipatory pursuit exist regardless of which feature of the stimulus is manipulated (speed versus direction) and over which time course both responses are compared (long-term prior versus shorter-term trial history).

Such opposite biases and different sensitivities to manipulations of motion signal strength in perception and pursuit are generally compatible with the idea of different information processing for both responses. Perception and visually-guided pursuit eye movements might rely on different information accumulation and integration over time, due to different needs of the perceptual and the oculomotor systems (Spering et al., 2011b). The current paper mainly compares perceptual responses to another aspect of pursuit, the earliest, anticipatory phase that is driven by cognitive, memory-related signals rather than by visual signals.

Interestingly, the present study did not find a significant effect of direction expectation on the later, visually-guided phase of smooth pursuit. However, in trials in which the perceived direction was incongruent with the physical motion direction (i.e., followed a repulsion bias), visually-guided smooth pursuit was aligned with perception. In the following paragraphs, we will discuss the characteristics of the signals driving motion perception and different phases of smooth pursuit with a main focus on anticipatory pursuit.

### **Different biases in motion perception and pursuit might reflect how both responses adapt to task requirements**

Studies on perceptual responses to manipulations in short-term or long-term probability have mostly revealed an attraction bias (Alais et al., 2017; Chalk et al., 2010; Kok et al., 2013), in which perception follows the recently viewed or most likely stimulus feature (direction, orientation, etc.). Our paradigm utilized short-duration displays and introduced a statistical bias of motion direction (long-term probability), similar to some of these studies (e.g., Chalk et al. 2010). However, we observed a repulsion bias. These different types of biases are interesting because they reveal that the perceptual system might respond to different task and stimulus environments in a flexible way, depending on the requirements of the task (e.g., to sensitively respond to a change or categorize information). A repulsion bias might reflect the need of the perceptual system to stay alert and to quickly respond to changes in the environment in an energy-efficient way: there is no need to be highly sensitive to a stimulus that always appears, whereas a novel stimulus would alert the system and may require priority processing. This is similar to the functional role of adaptation, yet results from Experiment 3 suggested that the repulsion perceptual bias in our experiment was not caused by low-level sensory adaptation.

Similarly, different result patterns in perception and pursuit might reflect different task requirements as well. Our results resemble those obtained in other studies comparing perception and pursuit (Spering and Gegenfurtner, 2007b), or pursuit and hand movements (Kreyenmeier et al., 2017). These studies found that pursuit generally followed the motion average of different target and context speeds, whereas perception and manual interception of a target followed the difference of target and background. Akin to the task requirements in our study, perception and action served different functions in these studies as well. Whereas perception's role appeared to be to segregate a target from the background, pursuit's role was to track in the general target direction in the presence of surrounding motion signals, resulting in motion vector averaging. In the present work the tendency for pursuit to rely on integration rather than segmentation of different signals seems to be extended to the trial-history domain, and to the anticipatory phase: integration of visual signals across many trials would drive anticipatory pursuit, whereas perception could be based on the contrast between the current visual input and long-term memory of visual motion. The latter is in line with the general idea that the signal reflecting the prediction error plays an important role for sensory perception (den Ouden et al., 2012). Accordingly, a weak signal of rightward motion in probe trials might have been considered as not rightward because it did not meet the expectation for strong rightward motion signals set by context trials.

### **Expectation effects on anticipatory versus visually-guided pursuit**

Anticipatory pursuit has been shown to be not purely habitual (Jarrett and Barnes, 2001, 2002; Kowler, 1989) but also sensitive to different types of cognitive cues and probabilistic context (Pasture et al., 2020; Santos and Kowler, 2017) as well as to reward (Damasse et al., 2018). In addition, we show that anticipatory pursuit velocity is modulated by motion coherence in context trials, i.e., motion signal strength in the prior history. Our results together with previous findings suggest that anticipatory pursuit is based on the integration of multiple signals, from low-level visual motion signals (weighted by the sensory strength, or saliency, e.g., RDK coherence) to higher-level cognitive cues such as expectation and reward. This holds across the short time-scale of a single trial for visually-guided early smooth pursuit (e.g., Ferrera and Lisberger 1997) and a much longer time-scale lasting several minutes for anticipatory pursuit, as in our experimental blocks. The assumption that anticipatory pursuit is based on such an integration of multiple signals is reasonable, considering that the goal of anticipatory pursuit is to reach accurate tracking as soon as possible, to reduce the temporal delay in tracking the visual target.

Interestingly, whereas anticipatory pursuit showed an attraction bias scaling with probability, late-phase visually-guided pursuit did not follow the same result pattern. This difference might be expected given that visually-guided pursuit and perception similarly rely on current sensory signals, whereas anticipatory pursuit is driven by expectation. Moreover, it is known that visually-guided pursuit and motion perception interact, and that motion perception can modulate pursuit (Madelain and Krauzlis, 2003; Montagnini et al., 2006). It is thus possible that the late-phase visually-guided pursuit observed in our experiment was driven by perception, regardless of the nature of the expectation information.

### **Neural correlates of expectation effects on perceptual bias and anticipatory pursuit**

The dissociation between effects of expectation on perception and anticipatory pursuit might be due to perception and pursuit depending on different cortical areas during different processing stages. For perception, modulation by expectation might have affected sensory processing of current stimuli, based on activity in early visual cortical areas. By contrast, anticipatory pursuit is not triggered by current stimuli but instead based on expectation or history, related to activity in frontal cortical areas. In the following paragraphs, we will discuss the neural correlates for perception and anticipatory pursuit accordingly.

Cortical area MT and the medial superior temporal area (MST) are the major sensory areas for motion processing for both perception and visually-guided smooth pursuit (Born and Bradley, 2005; Thier and Ilg, 2005). It is unclear which specific cortical areas are responsible for expectation effects on perception. However, there is evidence that modulation in early sensory cortices, from primary visual cortex (V1) to MT and MST, might underlie repulsion and attraction biases in perception. For example, the repulsion bias in perceived orientation was found to be stronger when the current and previous stimuli in a given trial were presented at the same location (Fritsche et al., 2020). These findings indicate that this orientation bias was driven by effects that are spatially specific (and retinotopically congruent), which likely implies modulation of neurons in early sensory cortex, such as V1, responsive to stimuli within small receptive fields. Similarly, spatial specificity has been found in visual motion adaptation in relation to neuronal activity

in area MT (Kohn and Movshon, 2003). Area MT is known for its large receptive fields and might inherit spatial specificity from V1 but also shows distinct adaptation responses (Kohn and Movshon, 2004) that could underlie a repulsion bias. Although our results indicate that such low-level sensory adaptation was unlikely the cause of the repulsion bias in our study, other mechanisms could have resulted in a similar modulation of MT neuronal activity, leading to a repulsion bias in perception. Congruently, for attraction biases induced by expectation, functional magnetic resonance imaging studies (e.g., Kok et al. 2013) showed that representation of visual motion direction in early sensory cortices from V1 to MT was biased toward the expected stimulus. Taken together, these studies indicate that sensory areas as early as V1, and potentially up to MT and MST, play an important role in the effect of expectation on motion perception. Whether the modulation on early sensory cortex comes from higher-level areas remains unclear.

The supplementary eye field (SEF) plays a critical role for anticipatory pursuit, as shown in studies using electrical microstimulation in SEF to elicit anticipatory pursuit (Missal and Heinen, 2004). Moreover, direction-selective neurons in area SEF showed stronger activity before anticipatory pursuit in their preferred direction, indicating that SEF plays a role in the preparation of anticipatory pursuit (de Hemptinne et al., 2008). The pursuit area of the frontal eye field (FEF<sub>SEM</sub>) could also contribute to anticipatory pursuit, because lesions in FEF could abolish the ipsilateral anticipatory initiation of pursuit (Macavoy et al., 1991), and the preparatory activity for eye movements of FEF<sub>SEM</sub> neurons could start more than 600 ms before target onset (Darlington and Lisberger, 2020), making it a good candidate to contribute to anticipatory movement commands. We hypothesize that expectation based on visual and/or motor history might be encoded in SEF and then combined with current sensory evidence in FEF (Darlington et al., 2018; Fukushima et al., 2013; Schall, 2015). The source of visual motion history might come from MT and MST, but the roles of these areas in anticipatory pursuit remain to be tested (Kowler et al., 2019).

### **Limitations and future directions**

One limitation of the current study is the use of different measurement metrics for perceptual and anticipatory pursuit responses, probabilistic on binary variables for the former and continuous for the latter. Different measurements might have different sensitivities and noise sources, making a correlation harder to be detected. This is a common issue in many studies comparing perception and eye movements, due to the distinct nature of the two types of responses (Cardoso-Leite and Gorea, 2010).

Another limitation due to the measurement metrics is that we were not able to analyze the temporal development of the expectation effect (i.e., dependence on trial history) for perception in detail. The relatively limited number of probe trials prevented us from finding reliable results when we further divided data into smaller samples depending on the recent trial history. Analyzing trial history dependence could potentially explain some sources of the difference, as anticipatory pursuit and perception have been shown to rely on history on different temporal scales (Maus et al., 2015). Attraction and repulsion perceptual bias seem to also operate on different time scales (Chopin and Mamassian, 2012; Fritsche et al., 2020) and could occur with slight changes of parameters in the same paradigm (Kanai and Verstraten, 2005). Therefore, understanding the temporal dependency and development of the effects of expectation would be crucial to

understand the complicated interaction between attraction and repulsion biases.

We do not know how robust our results are with regard to parametric variations of the visual stimuli, which might be the reason for observing a repulsion bias instead of attraction bias in perception. For example, an attraction bias is mostly observed in studies using moving stimuli whose directions differed by  $\sim 60^\circ$  or less (Fritsche et al., 2020) rather than  $180^\circ$  (as in our study). In addition, effects of expectation are often examined with weak motion stimuli, i.e., low contrast (Chalk et al., 2010) or low coherence (probe trials in our study), because the Bayesian integration hypothesis postulates that the effect of expectation would be larger on a stimulus with less reliable sensory signals. However, reducing coherence might introduce changes other than reducing contrast for RDK stimuli, such as inducing the perceptual phenomenon of motion transparency, in which two or more distinct surfaces are perceived as moving in different directions (Qian et al., 1994). Moreover, it is unclear which aspect of the motion signal is driving perception in our study. We did not assess speed perception and can therefore not rule out that speed signals might have affected perception irrespective of the coherence manipulation. Motion characteristics of noise dots in an RDK, together with their lifetime, affect the perception of global motion as well as pursuit quality (Pilly and Seitz, 2009; Schütz et al., 2010). We also did not directly test if or how much motion aftereffect would be reduced by reducing RDK coherence as the manipulation in Experiment 3, thus cannot completely rule out motion aftereffect as a cause for the perceptual bias. Future work is needed to elucidate the potential influence of the characteristics of sensory stimuli—ranging from simplified dots, blobs, and RDKs to more complex naturalistic stimuli (Goettker et al., 2020)—on behavioural biases in perception and eye movements.

Finally, the perceptual repulsion bias observed in our and other studies does not match predictions of optimal Bayesian integration. Standard Bayesian inference would predict an attraction bias to the prior. However, by combining this prediction with the efficient coding assumption that mutual information (Brunel and Nadal, 1998) between the actual stimulus value and the sensory measurement made by the observer is maximized, a new Bayesian observer model could account for the repulsion biases (“Anti-Bayesian” effects; Wei and Stocker 2015). In the future, this kind of modelling approach might help understand the complicated interaction between attraction and repulsion biases induced by experience-based expectation across different behavioural tasks.

## Chapter 5

# Discussion

In this dissertation, I examine how perception and eye movements process motion signals presented across space and time, and evaluate whether the underlying neural signal processing is associated or dissociated between the perceptual and oculomotor systems. Experimental designs included two types of eye movements: ocular torsion and smooth pursuit. These eye movements vary in the level of subcortical and cortical control, potentially implying different degrees of connection with perception. Torsion is mostly controlled by subcortical pathways, thus being more reflexive. Pursuit involves more signal processing in cortical areas and is more under voluntary control. In four series of experiments, I probed the relationship between perception and eye movements by manipulating visual motion signals and by investigating how the two responses utilize expectation based on past visual experience. I presented visual motion signals across space from small-scale, internal motion to large-scale, object motion. I manipulated expectation by presenting cognitive cues or by changing probabilities of past visual events. Taken together, these manipulations allow me to investigate the link between perception and action across different stimuli, tasks, and eye movement responses.

The work presented here yields the following key findings. First, the seemingly reflexive torsional eye movement response correlates with the strength of a perceived motion illusion. This observed association between ocular torsion and perception indicates that torsion might share early-stage motion processing with perception (Chapter 2.1). Anticipatory torsion can only be triggered by trial repetition, but not by cognitive cues that indicate the upcoming motion direction in the next trial (Chapter 2.2). This observation indicates that expectation signals are less effective in driving torsion, consistent with the fact that torsion is mostly controlled by subcortical pathways. By contrast, smooth pursuit is under more voluntary control, and is known to have a close link with perception (Schütz et al., 2011; Spering and Carrasco, 2015; Spering and Montagnini, 2011). In this dissertation, I show that pursuit reacts differently from perception when the task requires processing of diverse object and internal motion signals (Chapter 3), and when utilizing expectation from past visual experience (Chapter 4). These results indicate that pursuit and perception utilize higher-level motion and expectation signals differently, advancing our knowledge of the relationship between these

two key behavioural responses to visual motion in more complex situations.

In this chapter, I will discuss how this dissertation adds to our knowledge of the perception-action link by evaluating visual stimuli and task environments promoting perception-eye movement associations (Section 5.1) or dissociations (Section 5.2). In Section 5.3, I will discuss implications for neural mechanisms of perception-eye movement relationships. In Section 5.4, I will present potential implications for technology development and clinical practices.

## **5.1 Visual stimuli and task environments promoting perception-eye movement associations**

We live in a dynamic world and constantly interact with moving objects. Yet, the majority of studies examining the links between perception and action in the dual systems framework (Goodale, 2011; Milner and Goodale, 2008) used static stimuli. Observers in these studies were asked to either report or act based on the size, shape, or orientation of a stationary object (but see the double-step paradigm, e.g., Goodale et al. 1986). In this dissertation, I focused on perception and eye movements in response to visual motion. In this section, I will first discuss visual motion signals that promote associations between perception and eye movements.

Behavioural associations between perception and pursuit have been reported for experimental situations in which motion signals are largely unambiguous. These associations include similar sensitivity or response accuracy in motion detection or discrimination tasks, and are usually interpreted to imply common motion processing between perception and eye movements. For example, perception and pursuit show similar sensitivity and precision when discriminating motion of simple patterns, such as a translating single dot or grating (Gegenfurtner et al., 2003; Mukherjee et al., 2015; Osborne et al., 2007, 2005; Stone and Krauzlis, 2003). Similarities have also been found for more complex patterns that might include multiple motion signals, as long as an average motion signal can easily be extracted to inform perception and pursuit. For example, perception and pursuit show similar responses to RDKs, in which the average motion signal from multiple dots is relatively unambiguous (Mukherjee et al., 2015; Osborne et al., 2007; Watamaniuk and Heinen, 1999). In the aperture problem, veridical object motion can only be derived by combining motion signals from the whole structure, because local motion signals alone are ambiguous. However, local motion signals (motion of components of the object, e.g., one edge of a square) are dependent on the motion of the whole object (e.g., the square), and a combination of the local signals yields a coherent percept. Perception and pursuit still show similar biases and temporal response dynamics (Beutter and Stone, 2000; Born et al., 2010; Lorenceau et al., 1993; Masson and Stone, 2002; Stone et al., 2000). In this thesis, I show that the association between perception and eye movements extends to torsional eye movements (Chapter 2.1). When triggered by visual rotational motion of a large grating, torsion is correlated with perception. This finding provides additional evidence for common motion processing in perception and eye movements at an early processing stage (see Section 5.3). Taken together, perception and eye movements seem to show

associations when faced with motion signals that are simple patterns or form a coherent percept of the object.

## **5.2 Visual stimuli and task environments promoting perception-eye movement dissociations**

Although similarities and correlations are commonly observed between perception and eye movements, dissociations have also been reported (Spering and Carrasco, 2015). Specifically, dissociations appear to be triggered by situations that involve multiple ambiguous or independent motion signals within a scene, potentially creating task-uncertainty about which part of the scene to respond to. These multiple motion signals can come from different sources across space, such as target and background, or the target as a whole object and components within the target. Motion signals also occur across time, building up expectation about future stimuli. Dissociations when processing motion signals across space and time might reflect different functional demands between perception and eye movements, as summarized and discussed in Section 5.2.1 and 5.2.2. However, dissociations can also be due to methodological limitations leading to different temporal dynamics of the perceptual and eye movement measurements, which is discussed in Section 5.2.3.

### **5.2.1 Dissociations between perception and eye movements when processing motion signals across space**

When processing multiple signals within a scene, perception and action may utilize visual information differently based on their inherently different functional demands. In the classic dual visual systems framework, the discussion mainly focused on the comparison between perception of static objects and motor actions such as reaching and grasping (Goodale, 2011; Milner and Goodale, 2008). Perception strives to recognize and classify visual information, thus relying on the relative relationship of objects within the scene. The ability to segregate objects from visual scenes is essential for us to perceive the complex environment. The discussion of scene segmentation or figure-ground segregation dates back to Gestalt psychology, which describes rules of grouping visual stimuli that belong together (Koffka, 1920). In general, perception aims at segmenting a visual scene or segregating an object from its background, via a multistep process that involves processes sensitive to feature contrast and figure-ground boundaries (Roelfsema, 2006; Roelfsema and Houtkamp, 2011; Roelfsema et al., 2002). In contrast, motor actions such as reaching and grasping aim at interacting with the object. Therefore, instead of focusing on scene segmentation, they rely on the absolute coordinates with reference to the specific effector (e.g., how widely fingers should open to grasp an object; Goodale 2011; Milner and Goodale 2008).

In this dissertation, I examined motion perception and eye movements. Regardless of whether a stimulus is stationary or moving, the task of perception is still to evaluate the properties of a particular target. As a result, perception needs to segregate the moving target from other motion signals (Andersen, 1997; Braddick, 1993; Braddick and Qian, 2001; Britten, 1999; McOwan and Johnston, 1996). The need to segregate signals results in perception following the relative relationship of signals within a scene. In line with this theoretical

assumption, when a small moving target is presented against a large-field moving background, perception follows target speed relative to the background (contrast bias; Spering and Gegenfurtner 2007b). Moreover, an illusory component of target motion can be induced in the opposite direction of background motion (Zivotofsky, 2005), akin to the well-known induced-motion effect demonstrated by Gestalt psychologist Karl Duncker (Duncker, 1929). In contrast to these results, I found that perception on average is unbiased when observers were asked to judge object motion direction in the context of conflicting motion signals from within the object (Chapter 3, see also Hughes 2018). Observers may have ignored internal motion, because the task did not involve segregating the object from a complex scene or surround. Rather, the task focused on the object's trajectory. It could be argued that internal object motion is less relevant for a perceptual system that aims at segmenting a visual scene than diverse motion signals within an object. Interestingly, a further examination of individual data indicates that more than half of the observers tended to judge object motion relative to internal motion, revealing a contrast bias (Fig. 3.8). This response tendency was particularly pronounced for observers with a weak assimilation bias in their pursuit responses (Fig. 3.7). Observers with a strong assimilation bias in their pursuit responses, however, tended to judge the average motion of object and internal motion signals. Due to the ambiguity in the relationship between internal dots and the whole object, it is possible that observers had different interpretations of the task relevance of internal motion. Some observers might have considered the internal motion as noise or background (i.e., dots moving behind a translating aperture), from which the target motion should be segregated. Other observers might have considered internal motion as an intrinsic contributor to object motion (i.e., a translating and rotating object), and integrated both sources in perception and pursuit.

Eye movements, unlike reaching and grasping, do not directly interact with objects in the world. They serve to gather visual information and aid motor interactions with our dynamic visual environment (de Brouwer et al., 2021; Fooker et al., 2021). The eyes move to stabilize gaze and to shift the fovea—the area of highest visual acuity (Jacobs, 1979)—to an object location that maximizes visual information accrual. When multiple peripheral visual objects are shown, saccadic eye movements target the objects' centre of gravity (Findlay, 1982; Findlay and Gilchrist, 1997). During reading, the centre of a word is usually the ideal saccade target, if only one fixation is needed to recognize the word (Clark and O'Regan, 1999; Vitu, 1991). Similarly, when the eyes need to track a moving object in the presence of other motion signals, following the average motion direction or speed maximizes the ability to monitor and decode information from target and context. Rather than segregating moving objects or features from a scene or context as perception does, eye movements integrate all available motion signals. Congruently, smooth pursuit eye movements typically follow the average motion of different objects or scene components (e.g., Hughes, 2018; Lisberger and Ferrera, 1997; Masson et al., 1995; Niemann and Hoffmann, 1997; Spering and Gegenfurtner, 2007a,b). In line with these earlier findings, I also found that smooth pursuit followed the average motion of object and internal motion signals, showing an assimilation bias in all observers (Chapter 3).

To summarize, whereas perception and eye movements might rely on similar decoding of motion signals at an early processing level (e.g., Lisberger and Movshon, 1999; Newsome and Paré, 1988), they could

rely on different ways in which motion signals are computed at a later processing level, which takes into account object and scene information. When motion signals are simple and unambiguous, such as the large rotating grating presented in the study in Chapter 2.1, perception and eye movements are associated. When the relationship between diverse motion signals is ambiguous, perception and eye movements may be dissociated due to different functional demands. Perception focuses more on scene segmentation and signal segregation. If the diverse motion signals are all within the object as in the study presented in Chapter 3, perception of the object motion is overall not biased by internal motion, potentially because there is nothing that the object needs to be segregated from. Moreover, some observers might consider internal motion as the background, thus showing a contrast bias. However, eye movements focus on signal integration and show an assimilation bias when faced with diverse object and internal motion signals. Different response biases in this task could reflect activities of different types of motion-sensitive neurons in area MT (see Section 5.3). In the following section, I will discuss how different functional demands of perception and eye movements might be reflected by their dissociations when processing motion signals across time. Motion signals across time are manipulated by shaping expectation based on probabilities of past visual events (Chapter 4). The demand of perception to segregate motion signals is shown as a repulsion bias to past visual events, whereas the demand of eye movements to integrate motion signals is shown as an attraction bias to past visual events.

### **5.2.2 Dissociations between perception and eye movements when processing motion signals across time**

Our beliefs about future visual events are shaped either by implicit prior beliefs built on past experience (de Lange et al., 2018; Seriès and Seitz, 2013), or by explicit external events, such as visual cues. For example, a symbolic cue—an arrow presented in the screen centre—could indicate the direction of an upcoming motion stimulus. Cues could point to the location or time of an upcoming visual event and are generally known to enhance visual processing at the attended location, object, or feature (Carrasco, 2011). Implicit prior beliefs and explicit external cues require different levels of cognitive processing and might have different effects on perception and eye movements. In this dissertation, I compared how expectation based on experience, i.e., implicit prior belief, affected perception and eye movements.

Past visual experience is commonly integrated with current sensory signals. Past experience shapes a prior belief, also known as "a priori" as described by Bayesian inference models, which represents the expected probability of a future event (Maloney and Mamassian, 2009; Seriès and Seitz, 2013). The effect of this prior on perception is unclear in the literature. When one motion direction occurs more frequently than another, perception can be biased toward the more frequently shown direction (Chalk et al., 2010). This perceptual bias is often referred to as an "attraction bias". However, perception can also be biased against the direction of this prior, known as a repulsion bias (Fritsche et al., 2017; Maus et al., 2015; Zavitz et al., 2016). In Chapter 4, where probabilities of motion directions were manipulated, a repulsion bias was observed in perception. This finding is in line with the need of the perceptual system to identify a current object and to segregate it from past visual events. A novel stimulus may represent a potential threat in the environment,

thus should be given high priority in signal processing. Therefore, the perceptual system needs to stay alert to novel stimuli that are different from what has been observed in the past. This assumed process of segregating an object from within a stream of temporal occurrences is congruent with perceptual segregation of an object from within a spatial scene, as observed in Chapter 3. However, the repulsion bias observed in Chapter 4 is incongruent with the results of a previous study, in which the probability of motion direction was also manipulated (Chalk et al., 2010). These authors found a perceptual attraction bias in the direction of the most-frequently presented motion. Different stimulus properties and manipulations of motion ambiguity may have resulted in different perceptual response patterns among studies, because perception is sensitive to variations of stimulus parameters such as how noises are constructed in random-dot stimuli (Nawrot and Sekuler, 1990; Pilly and Seitz, 2009; Qian et al., 1994).

Across stimuli and tasks, eye movements always show an attraction bias to past visual events. Several studies have demonstrated that visually-guided smooth pursuit is biased towards the expected motion direction during pursuit initiation (Darlington et al., 2018, 2017; Kim et al., 2019). These findings extend to pursuit maintenance and catch-up saccades (Deravet et al., 2018), indicating a general principle of integrating past information with current sensory stimuli in sensorimotor processes. In addition, anticipatory smooth pursuit eye movements can be induced even before the onset of any visual stimuli, and consistently matches the expected motion direction and speed of an upcoming target (Chapter 4; Kowler 1989; Kowler et al. 1984; Maus et al. 2015; Santos and Kowler 2017). Interestingly, this strong effect of expectation extends to torsional eye movements, which can also be induced by expectation in the absence of visual signals (Chapter 2.2). This finding is particularly surprising, given that torsion is often considered reflexive and controlled mostly by subcortical areas. However, as anticipatory torsion cannot be induced by cognitive cues (Chapter 2.2), it might be controlled by different areas from the cortical areas controlling anticipatory pursuit (see Section 5.3). The consistency in expectation-induced eye movements might again reflect eye movements' functional demand of stabilizing gaze and integrating available motion signals. In this case, past visual motion signals are integrated across trials to inform eye movement direction and speed. The eyes start to move in the expected direction shortly before the onset of a visual target in order to catch up with the moving object as soon as possible once it appears. In this way, anticipatory eye movements can reduce retinal errors at the onset of visual stimuli and help with gaze stabilization.

### **5.2.3 Temporal dynamics of the perception-eye movement relationship**

In experimental psychology, perception is often operationally defined as a discrete judgment given at the end of a trial via a button press or similar responses. However, perception itself is not necessarily discrete. One perceptual decision made at the end of a trial cannot reflect the dynamics in our perceptual experience. To make a perceptual decision, observers can take time to accumulate all evidence and even process it after the stimulus display ends. Different from the perceptual response, eye movements are updated continuously throughout any given experimental trial. This is particularly the case for smooth pursuit eye movements, because these continuous movements require ongoing updating in response to changes in the visual environ-

ment. Therefore, differences in response sensitivity and accuracy between perception and eye movements could be due to differences in the amount of accumulated evidence under the same process, rather than being due to different processes (Cardoso-Leite and Gorea, 2010).

To address the limitation of measuring perception, we need a finer examination of the comparison between perception and eye movements across time. Specifically, perceptual responses would need to be probed at different time points. Some studies have measured perceptual responses with different display durations for simple stimuli such as dots or gratings, revealing similar temporal dynamics in perception and pursuit (Braun and Gegenfurtner, 2016; Mukherjee et al., 2015; Osborne et al., 2007, 2005). These observations suggest common motion processing between perception and pursuit, at least under certain stimuli and task conditions.

The temporal dynamics of the relationship between perception and pursuit in more complex stimulus and task situations, however, remains unclear. Across the different studies in this dissertation, I compared perception measured at the end of a trial to different phases of eye movements. For example, multiple motion signals can be processed similarly in perception and pursuit when considering the steady-state pursuit phase (close to when the perceptual judgment is given) as a point of comparison (Chapter 3, Fig. A. 1b). Congruently, steady-state or visually-guided pursuit is more closely aligned with perception in Chapter 4 than anticipatory pursuit (Fig. 4.6). Anticipatory pursuit is measured at the very beginning of a trial, long before a perceptual judgment is given. It is driven by distinctly different signals than visually-guided pursuit (Kowler, 1989; Santos and Kowler, 2017).

To elucidate the temporal evolution of the perception-eye movement link over time, perception would have to be measured during early phases of stimulus presentation. It remains unclear whether the alignment between perception and steady-state pursuit is due to common motion processing, or to a top-down perceptual modulation of pursuit. Common motion processing likely occurs during early stages as part of the feed-forward signals, whereas top-down perceptual modulation likely occurs later as feed-back signals. Because a perceptual decision measured after the conclusion of a trial might have been made at a point in time during stimulus display (Kiani et al., 2008), it remains possible that eye movements at later time points are affected by the perceptual decision once it is formed. If early-stage motion processing was shared, we would expect similar responses between early pursuit and perception with a shorter stimulus duration. If the correlation was caused by a top-down perceptual modulation, we may not find a similar relationship during early pursuit and perception with shorter stimulus durations.

In addition to the manipulation of stimulus duration, the temporal dynamics between perception and pursuit can also be probed by introducing time pressure. For example, the drift diffusion model describes the hidden process of evidence accumulation for decisions (Ratcliff and McKoon, 2008), which potentially corresponds to neural activities in cortical areas such as FEF (Heitz and Schall, 2012; Schall, 2019). By utilizing such models and manipulating speed accuracy trade-offs, the underlying processing of sensory evidence accumulation could be quantified for both perception and eye movements. When a perceptual decision has to be performed under extreme urgency, it is also possible to tease apart the early sensory and

late cognitive signal processing (Poth, 2021; Salinas et al., 2019; Shankar et al., 2011; Stanford and Salinas, 2021). Comparing the detailed temporal dynamics between perception and eye movements could yield a better understanding of how they are related or dissociated irrespective of the different temporal constraints of the measured responses.

### **5.3 Neural correlates of associations and dissociations between perception and eye movements**

In this section, I will discuss implications of the findings presented in this dissertation for our understanding of neural signal processing for perception and eye movements. From behavioural associations and dissociations, we may infer the stage at which the neural signal processing is shared or divided between perception and eye movements.

The main hubs for visual motion processing for both perception and pursuit are areas MT/MST (e.g., Dürsteler and Wurtz, 1988; Lisberger and Movshon, 1999; Newsome and Paré, 1988; Rudolph and Pasternak, 1999; Thurston et al., 1988). Although behavioural associations between perception and eye movements cannot confirm common processing, they can provide further evidence of the possibility of shared neural signal processing between perception and eye movements in areas MT/MST. For example, similar response patterns and temporal dynamics between perception and pursuit in motion discrimination tasks match MT neural activities, suggesting common processing of motion signals in area MT (Huang and Lisberger, 2009; Osborne et al., 2007; Pack and Born, 2001). In addition, studies have shown shared noise sources between perception and pursuit when discriminating both speed and direction of moving objects, consistent with the assumption that perception and pursuit share common sensory estimates in area MT (Mukherjee et al., 2015; Osborne et al., 2005; Stone and Krauzlis, 2003). However, other studies did not find a correlation of noise sources between perception and pursuit in speed discrimination tasks (Gegenfurtner et al., 2003; Rasche and Gegenfurtner, 2009). It remains unclear to what extent neural processing is shared between perception and pursuit, or if common processing depends on the dimension of motion being tested (speed vs. direction). In Chapter 2.1, I found a correlation between perception and torsion in response to large-field rotating gratings. This correlation might reflect common processing of large-field rotational motion in area MST for both perception and torsion, because neurons in the dorsal division of area MST have large receptive fields and are sensitive to visual rotational motion (Graziano et al., 1994; Mineault et al., 2012; Tanaka et al., 1989). Although it is unclear if area MST directly controls ocular torsion, the finding of a correlation between perception and torsion suggests such a possibility. In the brainstem, torsional quick phases are generated in the riMLF (Moschovakis et al., 1991a; Suzuki et al., 1995), and torsional eye position signals are generated in the INC (Crawford et al., 1991; Helmchen et al., 1998), which also contributes to torsional slow phases. MST directly projects to DLPN in brainstem (Boussaoud et al., 1992; Distler et al., 2002; Hoffmann et al., 2009; Ono et al., 2005), a pathway that carries eye velocity and visual motion signals and controls both smooth pursuit (Mustari et al., 2009; Ono et al., 2005) and OKN/OFR (Dürsteler

and Wurtz, 1988; Kawano et al., 1994; Takemura and Kawano, 2002). Connections between DLPN, riMLF, and INC (Noda et al., 1990) might then contribute to the cortical control of torsion from MST. Projections from MST to FEF then to riMLF (Lynch and Tian, 2006; Yan et al., 2001) and NRTP (Mustari et al., 2009; Ono et al., 2005; Ono and Mustari, 2009; Suzuki et al., 1999), and from MST to the pontine nuclei via NOT (Buttner-Ennever et al., 1996), might also contribute to the control of visually-induced torsion. NRTP contributes to the correction of torsional errors during saccades (Van Opstal et al., 1996), and NOT is crucial in generating the slow phases of OKN (Cohen et al., 1992; Kato et al., 1988; Masseck and Hoffmann, 2009).

Dissociations between perception and eye movements can imply differences in further processing of sensory and non-sensory signals along the pathways. In this dissertation, I examined how perception and eye movements process visual motion signals and expectation. Dissociations between perception and pursuit in response to visual motion signals across different spatial scales (Chapter 3) might indicate dependency on activities of different types of MT neurons. Studies have shown different types of MT neurons with either inhibitory or excitatory center-surround receptive fields, responding well to either small-scale or large-field motion (Allman et al., 1985; Born, 2000; Born and Tootell, 1992; Tanaka et al., 1986). These different types of MT neurons might be responsible for segregation and integration of diverse visual motion signals (Andersen, 1997; Born and Bradley, 2005; Britten, 1999). When processing motion signals across different spatial scales, perception might rely on the activity of neurons with inhibitory center-surround receptive fields to process relative motion signals, whereas pursuit might rely on the activity of neurons with excitatory center-surround receptive fields to process average motion signals.

Dissociations between perception and anticipatory pursuit (Chapter 4), and between anticipatory pursuit and anticipatory torsion (Chapter 2.2), might indicate distinct neural areas for processing expectation signals. Past visual events modulate activities in sensory areas such as V1 and MT, which could be responsible for both attraction and repulsion biases in perception (Fornaciai and Park, 2020; Kohn, 2007; Kok et al., 2013; Webster, 2015). Modulations in sensory areas might also come from higher-level areas, such as FEF, which projects to MT (Ninomiya et al., 2012; Ruff et al., 2008; Silvanto et al., 2006). FEF modulates visual spatial attention oriented by cognitive cues (Chanes et al., 2012; Chica et al., 2014; Taylor et al., 2007), thus might play a role in motion perception when expectation is induced by cognitive cues. However, it remains unclear whether FEF modulates MT activities based on experience. Anticipatory smooth pursuit, which does not depend on current sensory stimuli, is related to FEF/SEF activities (de Hemptinne et al., 2008; Macavoy et al., 1991; Missal and Heinen, 2004). Whereas FEF activities are mostly related to movement preparation, SEF activities are related to maintaining memory of target motion and interpreting decision rules for anticipatory pursuit (Fukushima et al., 2013; Yang and Heinen, 2014). Therefore, SEF seems to be the major area for planning anticipatory pursuit. Even if FEF is responsible for both perception and pursuit, it might play different roles when processing expectation based on past experience for perception and pursuit. The comparison between anticipatory pursuit and anticipatory torsion show that anticipatory torsion can be elicited by trial repetition, but cannot be elicited by cognitive cues (Chapter 2.2). This might indicate that anticipatory torsion is not controlled by frontal cortical areas, but by subcortical areas

such as the cerebellum, which plays an important role in motor learning (Ito, 2000). The flocculus and ventral paraflocculus have been shown to mediate adaptive changes in VOR (Hirata and Highstein, 2001; Rambold et al., 2002) and smooth pursuit (Kahlon and Lisberger, 2000; Medina and Lisberger, 2008). The cerebellum is also activated in anticipation of regular somatosensory stimulations, even when a stimulation was randomly omitted (Teschke and Karhu, 2000). Cerebellar activities related to oculomotor learning and sensory event anticipation might contribute to the generation of anticipatory torsion based on trial history.

To conclude, behavioural associations and dissociations suggest potential areas for shared or divided neural signal processing between perception and eye movements, although they do not confirm specific neural mechanisms. Instead, they provide implications about how each system processes different signals in the brain.

## **5.4 Practical implications**

Eye movements occur all the time and are highly relevant to perception and other motor actions. With the advantages of being easy to measure and quantify, having well-known physiology, and being related to functions beyond sensory processing, eye movements have already been widely used in applied and clinical settings (Shaikh and Zee, 2018). The understanding of the relationship between perception and eye movements can guide the development of novel technologies as well as applications in clinical practices.

### **5.4.1 Applied research for technology development**

The development of mixed reality displays is creating a new visual world. Augmented reality projects virtual information onto real scenes, whereas virtual reality creates a completely artificial environment for us to interact with. Although we cannot use eye movements to interact with the physical world, eye movements can be an efficient way of interaction in the virtual world. For example, selecting moving objects on artificial displays using hand movements can be challenging (Hasan et al., 2011; Mould and Gutwin, 2004; Ortega, 2013). Users usually need to point a cursor to the moving target and press a button to confirm the selection. Any mismatch between the target position during motion and the cursor position at the time of button press will result in inaccurate target selection (Hasan et al., 2011). Distractors and potential occlusion of the target in a complex environment can make the planning for target selection even harder (Mould and Gutwin, 2004; Ortega, 2013). However, it is possible to use eye movements for hand-free target selection (e.g., Khamis et al., 2018; Kytö et al., 2018; Luro and Sundstedt, 2019; Piumsomboon et al., 2017; Sidenmark et al., 2020). This type of interaction is natural and requires less cognitive load (Luro and Sundstedt, 2019). Using smooth pursuit to select moving targets in virtual reality can work effectively in tasks such as entering passwords and gaming (Khamis et al., 2018). The knowledge of how smooth pursuit performs in a more complex and naturalistic situation and how perception is related to smooth pursuit can help us develop new ways of interacting with the virtual world.

## 5.4.2 Clinical implications

Eye movements are impaired in a large number of diseases, such as neurodegenerative (e.g., Parkinson's disease and Alzheimer's disease; for reviews, see Anderson and MacAskill 2013; Pretegianni and Optican 2017) and psychiatric disorders (e.g., bipolar disorder and schizophrenia; for reviews, see Carvalho et al. 2015; Gooding and Basso 2008; Wolf et al. 2021). Because different types of eye movement deficits are linked to lesions affecting different brain areas (e.g., Barton, 2000; Barton and Sharpe, 1998; Barton et al., 1996; Pierrot-Deseilligny, 1994), the relationship between perception and eye movements can help us understand the mechanisms of deficits and the progression in such diseases. Depending on how eye movements are impaired, the source of perceptual deficits as well as the location of the impairment could be inferred. For example, patients with schizophrenia show deficits in predictive pursuit during temporary disappearance of moving objects, indicating insufficiency in using extraretinal signals for visual motion representations (Nagel et al., 2012; Thaker et al., 1999). This failure to utilize extraretinal signals for motion prediction could be related to disconnections among distributed neural networks (e.g., V5, lateral intraparietal area, SEF, and putamen; Nagel et al. 2012) and the general symptoms in schizophrenia (Bansal et al., 2018; Sperling et al., 2013). In contrast, Parkinson's disease patients show preserved predictive pursuit when visual motion is initially shown (Fooker et al., 2022; Helmchen et al., 2012), suggesting that these patients might have intact internal representation of visual motion. However, they show impairment in anticipatory pursuit when no visual motion has been displayed yet (Helmchen et al., 2012). This deficit in anticipatory pursuit could be related to the difficulty in movement initiation and potential damages in the frontal-basal ganglia pathway (Fooker et al., 2022; Helmchen et al., 2012). To conclude, by examining how perception and eye movements are impaired in different stimuli and tasks, we may further our understanding of the mechanism of diseases.

## 5.5 Conclusion

The main question to be addressed in this dissertation is to what extent perception and action share signal processing. Results from a series of studies indicate that perception and eye movements are likely to share early-stage motion processing, but differ in the further processing of both visual motion and expectation signals. These results are in line with the assumption that perception and eye movements have different functional demands. When motion signals are unambiguous or consist of simple patterns, perception and eye movements are associated. Such associations have been widely observed between perception and pursuit (Sperling and Montagnini, 2011). I show that the association can be extended to ocular torsion (Chapter 2.1), which is more reflexive and less under cognitive control (Chapter 2.2). However, when multiple motion signals across space and time are presented, dissociations between perception and eye movements are observed. The dissociations might reflect different functional demands of perception and eye movements. Perception adapts to the context and acts in service of object segregation. Congruently, we found an overall lack of bias in perception when diverse object and internal motion signals are presented (Chapter 3), and

a repulsion bias in perception induced by expectation based on past experience (Chapter 4). In contrast, eye movements follow the principle to maximize visual information accrual and perform signal integration. Therefore, smooth pursuit follows the average motion of diverse object and internal motion signals across space (assimilation bias; Chapter 3), and anticipatory eye movements are induced in the expected motion direction and speed (attraction bias; Chapter 2.2, 4). Overall, this dissertation provides further understanding of the perception-action link by examining how motion perception and eye movements are associated or dissociated.

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# Appendix: Further exploratory analyses between perceptual subgroups

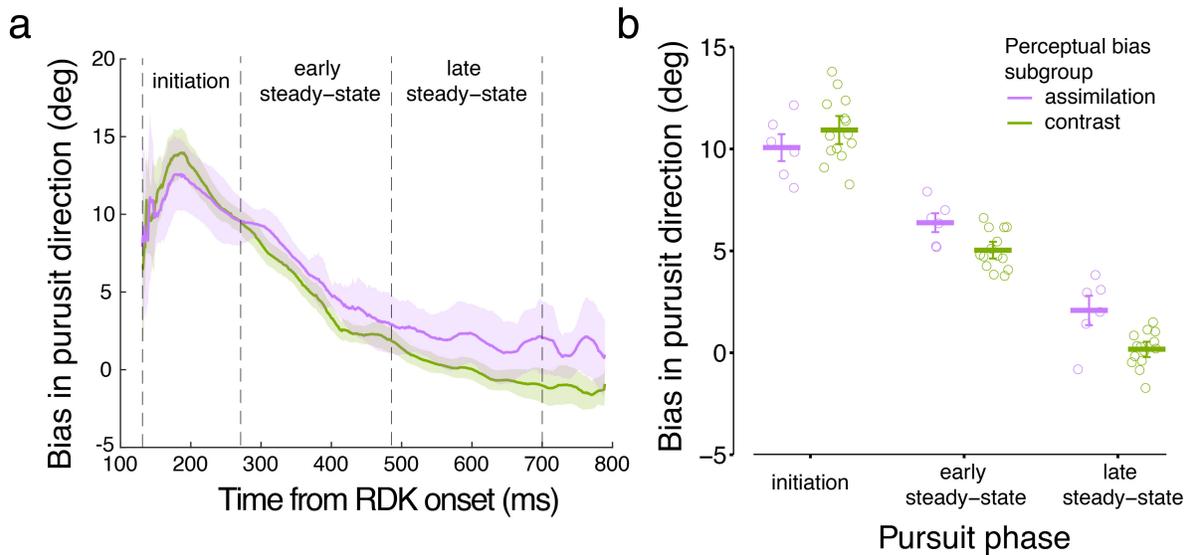
The following appendix provides details on the further exploratory analyses conducted in Chapter 3:

In the exploratory analyses, we showed that observers potentially have different perceptual bias patterns (Fig. 3.8). In addition, perceptual biases correlated with pursuit biases (Fig. 3.7). Because pursuit bias was dynamic and appeared to be stronger during the initial pursuit phase (Fig. 3.5a, b), we further explored whether observers with assimilation perceptual biases consistently showed a larger pursuit bias than observers with contrast perceptual biases over time. If observers with assimilation perceptual biases showed a larger pursuit bias consistently over time, it might reflect a general response tendency in these observers. By contrast, if the difference in pursuit bias between participants with different perceptual biases was developed during later pursuit phases, there might be a later perceptual modulation on pursuit. In addition, as the direct consequence of eye movements is the change in retinal image, we also examined how net motion energy of retinal image changed over time, and whether it differed between the perceptual subgroups.

## A.1 Temporal dynamics of pursuit bias between perceptual subgroups

To explore the temporal dynamics of pursuit bias in observers with different perceptual bias patterns, we calculated the average pursuit direction bias in three time windows (Fig. A.1a): the initiation phase (from pursuit onset to 140 ms after pursuit onset), the early steady-state phase (the first half of steady-state phase), and the late steady-state phase (the second half of steady-state). We conducted a two-way rmANOVA of pursuit bias with *subgroup* (assimilation and contrast) and *pursuit phase* (initiation, early steady-state, and late steady-state) as factors. We found that compared to the contrast group, the assimilation group had a slower decrease in pursuit bias over time (Fig. A.1b), indicated by a significant *subgroup*  $\times$  *pursuit phase* interaction effect [ $F(2,36) = 4.88$ ,  $p = 0.01$ ,  $\eta_p^2 = 0.21$ ]. Post-hoc  $t$ -tests with Tukey-adjusted  $p$  values showed that pursuit bias did not differ between the assimilation and contrast groups during the initiation [ $t(54) = -1.43$ ,  $p = 0.71$ , 95% CI of difference = (-2.66, 0.93)] and early steady-state [ $t(54) = 2.22$ ,  $p = 0.24$ , 95% CI of difference = (-0.45, 3.14)] phases. The assimilation group had a stronger pursuit bias than the contrast group only during the late steady-state phase [ $t(54) = 3.15$ ,  $p = 0.03$ , 95% CI of difference = (0.12, 3.70)]. In fact, some observers from the contrast group even showed a negative pursuit bias during

the late steady-state phase (Fig. A. 1b). Overall, the difference in pursuit biases between people having different perceptual bias patterns developed over time.



**Figure A. 1:** (a) Biases in pursuit direction in perceptual subgroups over time. Colour indicates the perceptual bias subgroup, see legends in panel (b). Solid lines indicate the mean pursuit bias in each subgroup. Shaded areas indicate the 95% CI. Dashed vertical lines indicate time points of the pursuit onset, and the start, middle point, and end of the steady-state phase analysis window. (b) Biases in pursuit direction in perceptual subgroups across the three pursuit phases. Horizontal bars indicate the mean across observers. Error bars indicate the 95% CI. Circles indicate the mean of individual observers. CI, confidence interval.

## A. 2 Net motion energy between perceptual subgroups

During eye movements, both retinal and extraretinal signals are required to recover the actual object motion in the world. As people with different perceptual biases tended to have various magnitudes of pursuit biases, it would be interesting to see how retinal image motion was affected. In several studies using RDK stimuli, a small proportion of observers perceived motion in the opposite direction of the RDK, even when the RDK had 100% motion coherence (Manning et al., 2022). The cause of such individual differences is unclear. One explanation is that even 100%-coherence RDKs could have motion energy (Adelson and Bergen, 1985) in the opposite direction (Bae and Luck, 2022; Manning et al., 2022). In the current study, motion energy of the retinal image may not directly correspond to pursuit direction biases, since the retinal image motion is affected by both speed and direction of the eyes. Therefore, we calculated the motion energy of retinal images over time, to examine whether motion energy of the stimuli could be a source of the diverse motion perception. If our stimuli contain motion energy in the opposite direction of internal motion, a diversity in perception might be encouraged.

We calculated the averaged bias in the net motion energy of retinal images for each observer across time. Specifically, for each trial, we first generated the 2D retinal image of the dots across time by subtracting the eye position from dot position on the screen in each frame. Then, two pairs of spatiotemporal filters were convolved with the retinal image to calculate the net motion energy over time. We adopted the demo code from Mather (2013) and used the spatiotemporal parameters detailed in a previous study (Kiani et al., 2008). Specifically, each pair of the spatiotemporal filter was the sum of different combinations of two spatial and two temporal filters. Each pair was selective for either the upward or the downward direction. The spatial filters were even and odd symmetric fourth-order Cauchy functions:

$$f_1(x, y) = \cos^4(\alpha) \cos(4\alpha) \exp\left(-\frac{x^2}{2\sigma_g^2}\right),$$

$$f_2(x, y) = \cos^4(\alpha) \sin(4\alpha) \exp\left(-\frac{x^2}{2\sigma_g^2}\right)$$

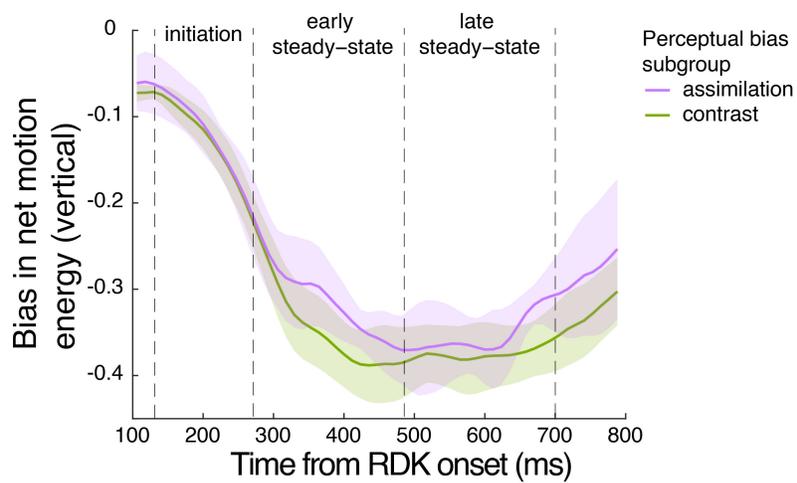
where  $\alpha = \tan^{-1}(y/\sigma_c)$ ,  $\sigma_c = 0.35^\circ$ , and  $\sigma_g = 0.05^\circ$ . The half width of the spatial filters was  $0.7^\circ$ . Two temporal filters were defined by the following functions:

$$g_1(t) = (60t)^3 \exp(-60t) \left[ \frac{1}{3!} - \frac{(60t)^2}{(3+2)!} \right],$$

$$g_2(t) = (60t)^3 \exp(-60t) \left[ \frac{1}{5!} - \frac{(60t)^2}{(5+2)!} \right]$$

The duration of the temporal filters was chosen to be nine frames, about 106 ms. Since the pursuit latency was  $132 \pm 13$  ms in the current study, 106 ms was roughly enough time to gather information for pursuit planning/updating. It was also comparable to the temporal filter length used in a previous study for pursuit and perception (Mukherjee et al., 2017).  $f_1g_1 + f_2g_2$  and  $f_1g_2 - f_2g_1$  (element-wise multiplication of  $f$  and  $g$ ) would pass information in the upward direction, whereas  $f_1g_2 + f_2g_1$  and  $f_1g_1 - f_2g_2$  would pass information in the downward direction. After convolving each filter with the 3D spatiotemporal retinal image pattern, the results of each pair were squared and summed up to calculate the motion energy in the upward and downward direction separately. Then, motion energy in the downward direction was subtracted from that in the upward direction to yield the net motion energy.

The net motion energy was normalized between  $-1$  and  $1$ . A positive bias value indicates more motion energy in the internal motion direction. Surprisingly, we found that our stimuli contained slight motion energy in the opposite direction to internal motion, as shown by the negative bias values during the initial duration before pursuit onset (Fig. A. 2). With the eyes moving, more motion energy in the opposite direction was observed. The net motion energy of retinal images did not seem to differ between perceptual subgroups, although there seemed to be a trend that the net motion energy of retinal images for the assimilation group is less in the opposite direction to internal motion (Fig. A. 2).



**Figure A. 2:** Biases in net motion energy in the vertical dimension between perceptual subgroups. Positive values indicate that there was more motion energy in the same direction as internal motion. Solid lines indicate the mean of each perceptual subgroup. Shaded areas indicate the 95% CI. Dashed vertical lines indicate time points of the pursuit onset, and the start, middle point, and end of the steady-state phase analysis window. CI, confidence interval.