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Publication Date

2026-05-01

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Misperceptions of Motion During Visual Fixation and Smooth Pursuit

by

Josephine Cordelia D'Angelo

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Vision Science

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Austin Roorda, Chair

Professor Jorge Otero-Millan

Professor Jacob Yates

Spring 2026

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Josephine Cordelia D'Angelo

Abstract

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It has long been known that humans are exquisitely sensitive to detecting relative motion; motion of one object relative to a fixed frame of reference. This discriminative ability is considered a hyperacuity because detection thresholds are smaller than the spacing between photoreceptors. Yet, when an image moves in a direction that is directly opposite to the direction of eye motion; in a direction consistent with retinal slip, it appears relatively stable despite the presence of world-fixed background content. It is not known how the visual system leverages frames of reference and the magnitude of retinal slip in governing perception of motion when images move in a direction consistent with retinal slip. Further, it remains unknown whether this phenomenon exists during other eye movements, such as smooth pursuit, when a subject tracks a moving target. We measured motion perception during visual fixation and smooth pursuit eye movements. We used an adaptive optics scanning light ophthalmoscope to track fixational eye movements; and we used a custom-built binocular eye tracker to track smooth pursuit eye movements. Our results show how the direction with which objects move contingent to fixational and smooth pursuit eye movements, gives rise to perceptions and misperceptions of motion.

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Acknowledgments

First and foremost, I thank my advisor, Austin Roorda, for his support throughout my Ph.D., for consistently pushing me beyond my comfort zone, and for encouraging me to approach research with rigor and curiosity.

I express my heartfelt gratitude for the mentorship of Jorge Otero-Millan, whose guidance and feedback were invaluable in developing my research. I thank my dissertation committee member, Jacob Yates, whose feedback strengthened each of my projects. I thank my qualifying exam committee member, Susana Chung, for pushing me to deepen and defend my understanding of vision science. I thank Marty Banks and Emily Cooper for their helpful discussions and valuable feedback during lab meetings.

I am grateful for the collaborations that have supported my research throughout my Ph.D. I thank my collaborators at Montana State University, David Arathorn and Raymond J. Weber, for their insights and guidance. I thank my collaborators from my internship project, with special thanks to my manager, Phil Guan.

I have been fortunate to work alongside lab mates from whom I have learned a great deal over the years. I thank the current and former members of the Roorda lab: Pavan Tiruveedhula, James Fong, Jason Wong, Leah Johnston, Shangbang Luo, Charlotte Wang, David Merino, Gareth Hastings, Norick Bowers, Alexandra Boehm, John Erik Vanston, and William Tuten. I thank my lab mate from the Otero-Millan lab, Evalie Rehor. A special thank you to my lab mate and closest friend, Hannah Doyle, whose friendship and constant support made the challenging moments feel manageable and the best moments all the more meaningful.

I am grateful to my friends, whose encouragement and companionship throughout my Ph.D. have helped shape both my journey and the person I have become: Leyla Kabuli, Tiffany Chien, Nikita Gaurav, Matangi Kumar, Sonali Singh, Vicki Kuo, Ângela Tomaz, Pabita Dhungel, Galen Chuang, Ben Chin, Avi Aizenman, Angelica Godinez, and Vasha DuTell.

Most importantly, I thank my family for their love and encouragement, especially to my Aunt Janis, Aunt Donna, Uncle Robbie, and Uncle Denis. And most of all, I am thankful to my siblings for their lifelong love and support: Luke, Evelyn, Rosey, John Gabriel, Mark, Mary, Elisa, Maximilian, and I remember with love Annie and Michael.

Chapter 1

Introduction

Vision is a dynamic process, the eye is ever moving as a person observes and interacts with the world. When a person wishes to look at an object, they move their eyes so that the light from the object lands onto the fovea of each eye, the area of peak photoreceptor density. The light is captured by these light-sensitive cells, transformed into an electrical signal, and sent to the visual cortex to generate percepts.

To maintain a high resolution percept, the eye would attempt to stabilize the image onto the fovea, but if the eye ever achieves perfect stability, the image will quickly fade from view [19, 69]. The eye therefore is in constant motion, whether fixating a world-stationary object or tracking a moving target. Yet, the visual system in general perceives both stationary and moving objects veridically.

This dissertation focuses on the relationship between eye movements and motion perception. We combine eye tracking with retina-contingent stimuli to investigate how the movement of images across the retina (retinal slip) gives rise to perceptions and misperceptions of motion.

Fixational Eye Movements.

When we try to fixate our eyes onto a stationary target, they make continuous miniature movements called fixational eye movements [18, 44, 67, 75]. Fixational eye movements have been categorized into three main types: tremor, high-frequency jitter with amplitudes that are on the order of a few arcseconds [10]; microscaddes, small and ballistic movements that occur approximately 2-3 times per second; and drift, a slow random motion that occurs between microscaddes [44, 75]. The amplitudes of fixational eye movements are large enough to make details of the scene sweep across the retina by a detectable amount, yet we are not aware of these eye movements and in general humans perceive a stable world. The human visual system evolved to discount the image motion owing to eye motion, and even leverages its motion to improve spatial vision [68, 76].

Humans Are Exquisitely Sensitive to Relative Motion.

The most sensitive judgments of motion require the presence of a world-fixed reference object near the moving target, like detecting a moving satellite among the stars or a bug crawling across a tree trunk. In a study exploring this discriminative ability, Legge and Campbell [42] found that in conditions with a frame of reference, displacement thresholds were as low as 0.3 arcminutes. By comparison, the center-to-center spacing of foveal cones is approximately 0.5 arcminutes [86]. Detecting relative motion is therefore considered a hyperacuity, which is a class of visual tasks where the motion or displacement detection thresholds are smaller than the sampling limits of the photoreceptors [88]. In the absence of a frame of reference, motion judgments are impaired [50, 42].

A Condition Where Humans Are Insensitive to Relative Motion.

There are at least three reports of a special condition under which humans fail to accurately detect relative motion. Riggs et al. [70] used an optical lever technique to either stabilize the retinal image or to amplify the retinal slip. They reported that under the amplified conditions, stimuli appeared to be “locked in place.” The authors never quantified the perceived motion under these amplified conditions nor did they ever do follow-up studies on this observation. Years later, Arathorn et al. [5] found something similar when they used an eye-tracking and stimulus-delivery system to directly project images onto the retina in a retina-contingent manner. They found that under conditions where the retinal slip was unnaturally amplified, the retinal image appeared stable, despite the presence of unavoidable, world-fixed retinal background content that might have served as a frame of reference. Turano and Heidenreich [83] explored the detectability of changes in the motion of a sinusoidal grating while the subject pursued a simultaneously presented smooth pursuit stimulus that moved faster or slower than the grating. When the smooth pursuit stimulus moved slower than the grating, the subjects exhibited an expected sensitivity to differences in grating motion. However, when the smooth pursuit target moved faster than the grating, the subjects exhibited an unexpected difficulty detecting changes in the grating motion. In all three reports, the images on average moved in a direction consistent with retinal slip, resulting in an impaired ability to detect relative motion.

1.1 Methods for Chapters 2 and 3

In the following studies presented in Chapters 2-4, we investigate this “illusion of relative stability” for all images moving in the direction of retinal slip. In Chapters 2 and 3, we present retina-contingent stimuli using an adaptive optics scanning light ophthalmoscope and we perform statistical analyses to quantify fixational drift and motion perception. These methods are described here:

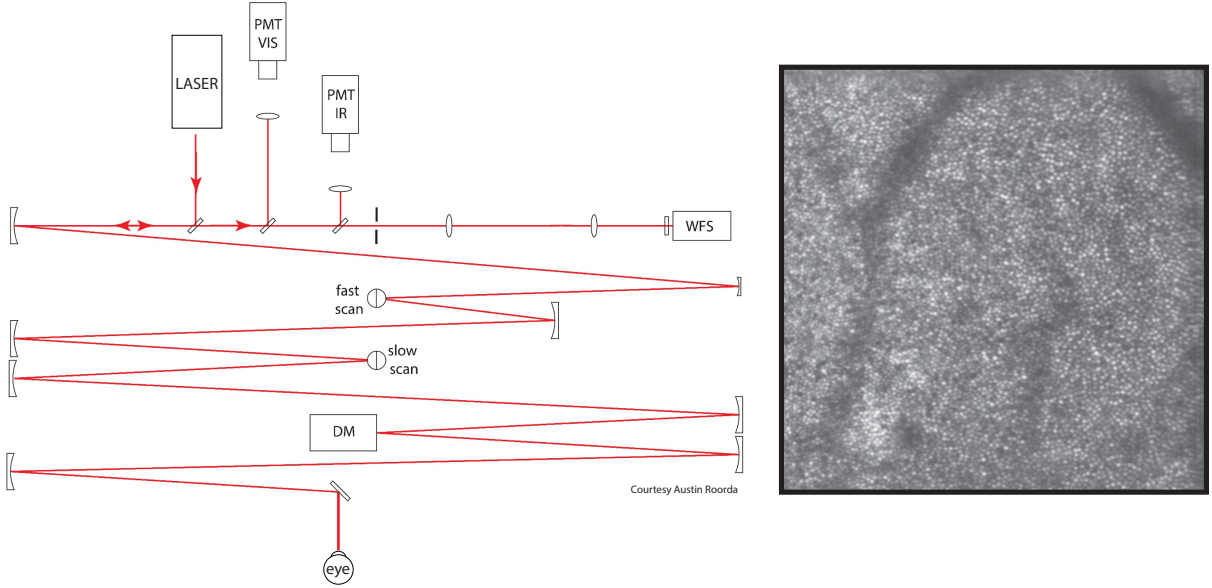


Figure 1.1: Schematic of the adaptive optics scanning light ophthalmoscope and an example image of a retina. (Left) Light from a supercontinuum laser is split into 3 independent channels that are aligned to travel along the optical path that is shown in red. (Right) Retinal mosaic obtained at a retinal eccentricity of 2° temporal to the fovea. The field of view corresponds to a 1.71° raster scan.

Adaptive Optics Scanning Light Ophthalmoscopy.

Retinal imaging and stimulus delivery were performed using a multiwavelength AOSLO [54, 74]. Light from a supercontinuum laser (SuperK Extreme; NKT Photonics, Birkerød, Denmark) was split into 3 independent channels. The 940-nm wavelength was used to continuously measure the optical imperfections of the eye, which were corrected with a deformable mirror (DM97-08; ALPAO, Montbonnot-Saint-Martin, France), enabling near diffraction-limited resolution. The 840-nm wavelength imaged a 1.71° field of the retina. The image was formed pixel by pixel, by measuring the scatter light from the focused spot as is raster-scans across the retina. The 680-nm wavelength was modulated by an acousto-optic modulator (AOM) to deliver the stimuli and we used custom software to move the stimuli contingent to the retinal motion [6]. The system had a frame rate of 60 Hz and a fast horizontal scan rate of ~ 16 kHz, rendering 512 by 256 pixel video recordings. Each pixel subtended 0.2 by 0.4 arcmin of visual angle. Fig. 1.1 shows a schematic of the AOSLO and a representative image of the retina.

In Chapter 2, the AOM modulated a 680-nm laser beam to deliver a circular 12-arcminute-diameter increment stimulus onto targeted retinal locations. Concurrently, the AOM modulated the 840-nm imaging beam to turn off at the same targeted retinal locations. This rendered a 3×3 arcminute decrement in the image which enabled unambiguous tracking

of the 680-nm increment stimuli. The average powers of the 940-nm, 840-nm, and 680-nm lasers were $50.3 \mu\text{W}$, $110.1 \mu\text{W}$, and $3.53 \mu\text{W}$, which correspond to equivalent luminance values of 0.0031 cd/m^2 , 0.83 cd/m^2 , and $1,200 \text{ cd/m}^2$ using methods described in Domdei et al. [21].

In Chapter 3, the AOM modulated a 680-nm laser beam to deliver three independent stimuli. This was possible by updating the FPGA board to allow up to three retina-contingent stimuli, rather than one. This new feature was an upgrade from Chapter 2 [17]. The average power of the 940-nm, 840-nm, and 680-nm laser beams were $58.6 \mu\text{W}$, $111.4 \mu\text{W}$ and $11.6 \mu\text{W}$ giving rise to equivalent luminances of 0.0036 cd/m^2 , 0.84 cd/m^2 and 3960 cd/m^2 using methods described in Domdei et al. [21].

Real-time Eye Tracking.

When imaging with an AOSLO, eye movements expand, compress, or distort the retinal images [81]. To mitigate these effects, the system recovers and then corrects for the eye movements in real-time. This is achieved through the following: At the beginning of the experiment, the experimenter selects a reference frame. During the experiment, as the 512 by 16 pixel strips are acquired by the fast horizontal scanner, they are registered to the reference frame. The x and y offsets necessary for best registration are measures of the absolute eye movements during the recording [6].

Targeted Stimulus Delivery.

By recording the eye motion in real-time, the AOSLO can perform targeted stimulus delivery. As the 840-nm laser images the retina and the system recovers the eye motion in real-time, an AOM arms the 680-nm laser to deliver stimuli that move contingent to eye motion [6]. These stimuli are called “retina-contingent stimuli”. The use of narrow strips for registration combined with fast processing, enables a ~ 2 -ms lag between eye motion prediction and stimulus delivery [81, 82, 89]. The specific Gains used for each study are described more fully in Chapters 2 and 3.

Statistical Analyses of Fixational Eye movements.

Random Walk Analysis.

Fixational drift, the eye motion that occurs in between microsaccades, resembles a random trajectory similar to Brownian motion [14, 16, 17, 22, 24, 41, 51, 71]. That is, the motion is two-dimensional with a velocity that varies according to a normal distribution. Studies have shown, however, that drift deviates from uncorrelated random motion, instead having correlated or anticorrelated properties depending on the timescale [16, 17, 22, 24]. To quantify the statistical properties of drift, we computed the diffusion constant (D) which quantifies the amount the eye moves from its starting position as a function of time, and we computed the α which measures the extent to which the steps in the trajectory are uncorrelated, positively

correlated, or negatively correlated. Equation 1.1 shows a method to solve for the diffusion constant and the scaling exponent α [15, 65].

$$MSD(\Delta T) = 2dD\Delta T^\alpha \quad (1.1)$$

We evaluated the mean square displacement (MSD) as a function of multiple time intervals (ΔT), to determine the magnitude of drift (D) and the extent to which the drift statistics deviate from Brownian motion (α), by fitting the model shown in Equation 1.1 to the empirical. The MSD is the squared Euclidean distance of the horizontal and vertical positions of the eye between two time points specified by the ΔT (Equation 1.2). The ΔT are the times between 1 frame (~ 17 milliseconds), 2 frames (~ 33 milliseconds), 3 frames (~ 50 milliseconds), and so on. The dimension (d) is equal to two because we recorded the x and y positions of the eye. As expressed in Equation 1.2, we computed the MSD over nonoverlapping ΔT 's. Overlapping pairs are highly correlated, and therefore computing over nonoverlapping pairs aimed to mitigate accidentally biasing the α to higher values. This was primarily important when computing over a low number of traces. As suggested by Saxton [78], the number of ΔT 's was determined by one-quarter times the total time steps (in our case, total number of frames). We did not calculate beyond one-quarter of the time steps because higher ΔT 's have fewer samples and are thus more vulnerable to noise [78]. In Equation 1.2, N represents the total time steps and $\lfloor \cdot \rfloor$ represents the greatest integer function.

$$MSD(\Delta T) = \frac{1}{\lfloor N/\Delta T \rfloor} \sum_{j=1}^{\lfloor N/\Delta T \rfloor} ((x_{j\Delta T+1} - x_{j\Delta T-\Delta T+1})^2 + (y_{j\Delta T+1} - y_{j\Delta T-\Delta T+1})^2) \quad (1.2)$$

From Equation 1.1, if $\alpha = 1$, then the MSD increases linearly with ΔT . This is uncorrelated random motion because the steps in the trajectory are independent from previous steps. This is referred to as Brownian motion. When $\alpha > 1$, the MSD increases faster than linearly with ΔT . The steps in the trajectory are positively correlated; each step has a tendency to continue moving in the same direction as the previous step. This is referred to as superdiffusion [33], persistence [15, 22, 43], or diffusion with flow [65]. When $\alpha < 1$, the MSD increases slower than linearly with ΔT . The steps in the trajectory are negatively correlated; each step has a tendency to move in the opposite direction as the previous step. This is referred to as subdiffusion [33], antipersistence [15, 22, 43], or caged motion [65]. In this dissertation, we use the terms Brownian motion, persistence, and antipersistence.

We compute the diffusion constant and α by plotting the $\log_{10}(\text{MSD})$ as a function of the $\log_{10}(\Delta T)$. The slope of the line across these data points is α and the y-intercept is $\log_{10}(\text{diffusion constant})$. Therefore, across all traces from each analysis, we quantified the amount of motion (diffusion constant) and its deviation from Brownian motion (α). Examples graphs are shown in Fig. 1.2 A–C.

Speed Analysis.

We additionally quantified eye motion by computing the speed. Across all traces with retina-contingent stimulus presentation, we computed the average displacement of the eye per frame. In both studies presented in Chapters 2 and 3, eye positions were sampled at 60 Hz.

1.2 Simulating Random Walks

This section describes the analyses of simulated random walks for the purpose of 1) understanding the implications of α and 2) justifying the need for a sufficient number of traces.

We simulated 20 antipersistent (Fig. 1.2A, $\alpha = 0.68$), 20 Brownian (Fig. 1.2B, $\alpha = 1.01$), and 20 persistent (Fig. 1.2C, $\alpha = 1.90$) random walks. The motion traces are shown in Fig. 1.2 below the graphs. The white crosses indicate the starting position for each trace.

Generating Random Walks with Varying α 's and Diffusion Constants.

These traces were generated by computing randomized step lengths in x and y drawn from a normal distribution with a standard deviation equal to 1 arcminute per step. For the sake of brevity, we will refer to the standard deviation of the randomized step lengths as simply *step lengths*. We converted the step lengths to polar coordinates to obtain the 2-dimensional step. Next, we selected the angle. All angles were equally probable for the first step.

- When generating traces with α less than one, for all subsequent steps, each angle was drawn from a normal distribution with a mean equal to the angle of the previous step subtracted from 180° and with a standard deviation determined by the α (Fig. 1.2A). As the α decreased below one, the standard deviation of the angle became smaller.
- When generating traces with α equal to one (Fig. 1.2B), all angles were equally probable for all subsequent steps.
- When generating traces with α greater than one (Fig. 1.2C), for all subsequent steps, each angle was drawn from a normal distribution with a mean equal to the angle of the previous step and with a standard deviation determined by the α . As the α increased beyond one, the standard deviation of the angle became smaller.

After generating all 2D steps and angles for the particular duration (1.5 seconds or 90 frames), we converted back to Cartesian coordinates by taking the cosine and sine of the angles and multiplying by the 2D steps to determine the x and y positions, respectively. The positions were successively added to generate the trajectory.

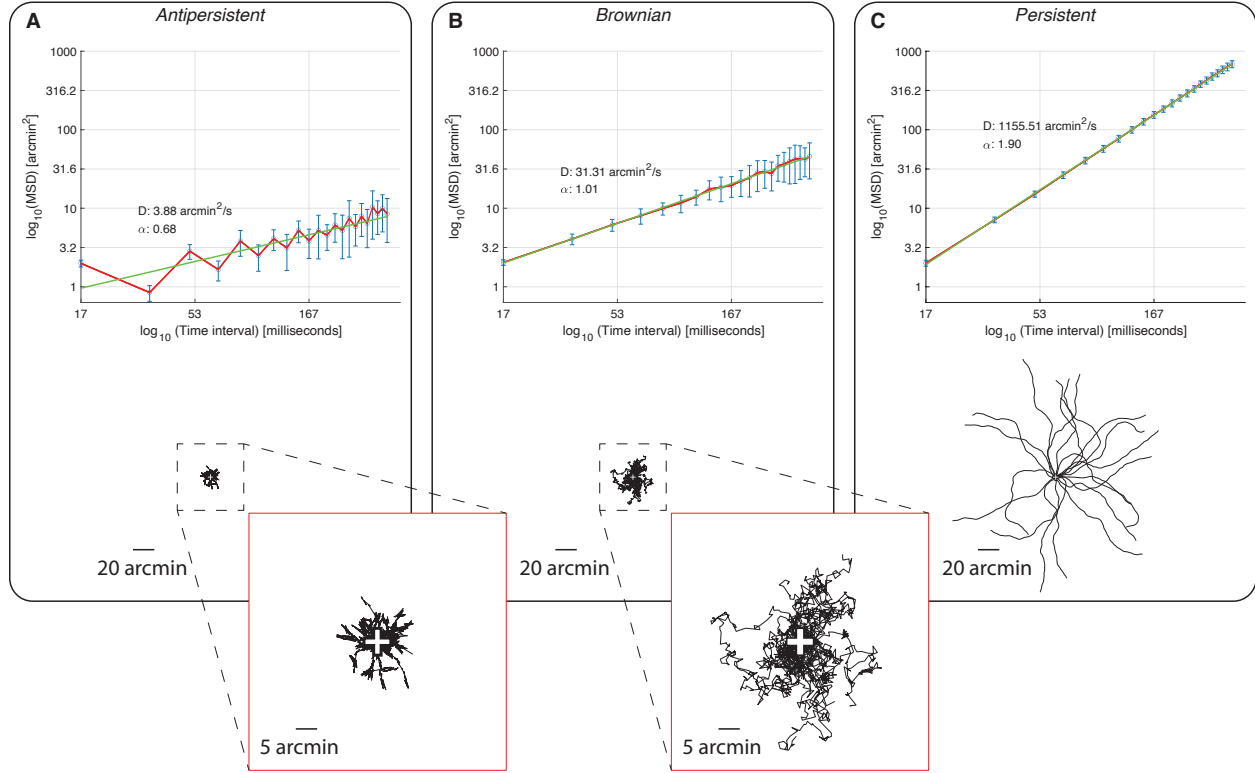


Figure 1.2: Examples of simulated random walk analyses and traces: 20 antipersistent (A), 20 Brownian (B), and 20 persistent (C). All traces were generated with randomized step lengths in x and y drawn from a normal distribution with a standard deviation equal to 1 arcminute per step, and the total duration was 1.5 seconds (90 frames). In the top graphs, the blue points represent the average $\log_{10}(\text{mean square displacement})$, or $\log_{10}(\text{MSD})$, computed over the 20 traces with SD bars. We interpolated points between the $\log_{10}(\text{MSD})$ to ensure uniform weighting for each position on the $\log_{10}(\text{time interval})$ axis, shown in red. The green line represents the best-fit to these interpolated points, from which we determine the slope (α) and y-intercept $\log_{10}(\text{diffusion constant})$. The time intervals (ΔT) are the times between 1 frame (~ 17 milliseconds), 2 frames (~ 33 milliseconds), 3 frames (~ 50 milliseconds), and so on. The motion traces are shown below with zoomed-in views outlined in red. The white crosses indicate the starting position for each trace.

How α Impacts the Random Walk.

This process of generating random walks effectively randomized the length of each step. The direction was also randomized; however, as α deviated greater than one, the trajectory more likely moved in the same direction as the previous step (Fig. 1.2C); and, as α deviated less than one, the trajectory more likely moved in the opposite direction of the previous step (Fig. 1.2A). In Fig. 1.2, observe how: 1) the slopes get steeper from A to C since α is determined by the slope; 2) even though all traces were generated with the same step length, 1 arcmin, the different α 's gave rise to different motion statistics; and 3) the diffusion constant is dependent on α : given the same step length, higher α 's give rise to higher diffusion constants. These characteristics and possible implications on the analysis are described further in Chapters 2 and 3.

How Many Traces Should You Analyze to Accurately Determine the Diffusion Constant and α ?

Owing to the random nature of generating traces in this method, the same randomized step length could generate a trace with a range of possible diffusion constants and α 's. For example, in Fig. 1.2, for each graph we simulated 20 traces and computed the average $\log_{10}(\text{MSD})$ across the 20 traces. However, one could compute a diffusion constant and α from a single trace. Fig. 1.3A plots the diffusion constants vs α computed from each of the 20 traces for the three simulations: antipersistent (blue), Brownian (orange), and persistent (purple). The hollow black points represent the diffusion constant and α computed from the average $\log_{10}(\text{MSD})$. Some of the diffusion constant's and α 's lie close to the black hollow points while others deviate significantly. This is why it is important to compute these parameters over multiple traces. In the context of eye motion, suppose you collected multiple 1.5-second duration recordings of drift motion. The individual traces could have a range of diffusion constants and α 's, but when you measure the average $\log_{10}(\text{MSD})$ across all the traces, you obtain an approximation that better represents the overall average motion statistics. How many traces are sufficient?

To address this question, we generated 100 Brownian random walks with an average step length equal to 1 arcmin and duration equal to 1.5 seconds (90 frames), using the same method used in Fig. 1.2B. Then we computed the diffusion constant and α from the $\log_{10}(\text{MSD})$ of the first trace; from the average $\log_{10}(\text{MSD})$ of the first and second traces; from the average $\log_{10}(\text{MSD})$ of the first, second, and third traces; and so on up to 100. We repeated this procedure 100 times, each time with a new set of 100 simulated Brownian random walks. These diffusion constants and α 's are shown in Fig. 1.3B vs the number of traces used to compute the average $\log_{10}(\text{MSD})$. Each point is the average of 100 simulations with SD bars. The true diffusion constant and α values used to generate these traces are indicated by the green lines, 30 arcmin²/s and 1, respectively. From these simulations, we suggest using at least 20 traces ($SD_{\text{Diffusion constant}} = 3.62$ & $SD_{\alpha} = 0.031$) to approximate the diffusion constant and α , but more traces are recommended.

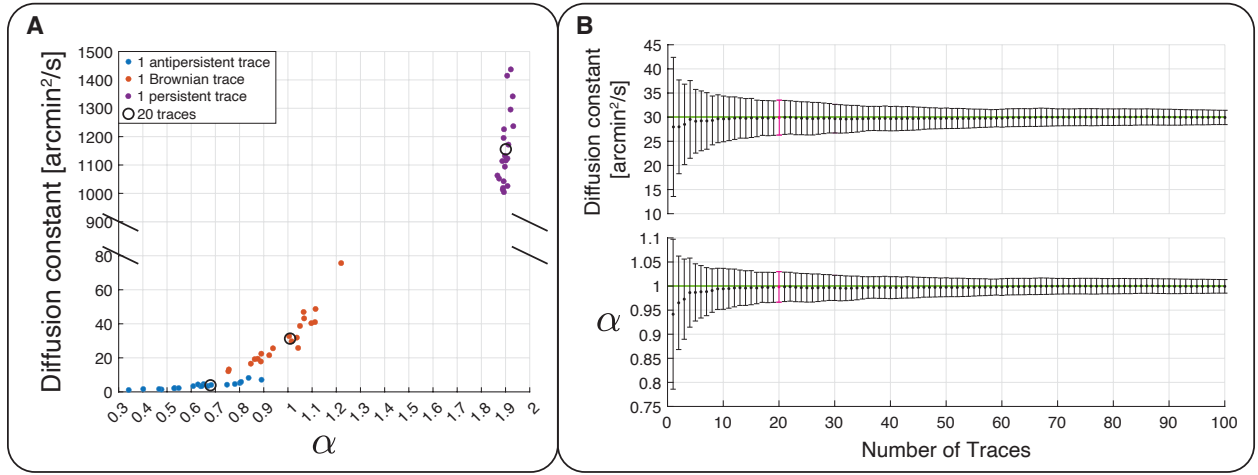


Figure 1.3: Examples showing how diffusion constant and α vary with number of traces. (A) The blue, orange, and purple points indicate diffusion constant's and α 's from individual antipersistent, Brownian, and persistent traces, respectively. The hollow black points represent the diffusion constant and α computed from the average $\log_{10}(\text{mean square displacement})$ ($\log_{10}(\text{MSD})$) (Fig. 1.2). Although all traces were generated with a 1 arcmin step length and 1.5 second duration, the randomness inherent in this method produces traces with a range of possible diffusion constants and α 's. (B) Diffusion constants and α 's computed from the $\log_{10}(\text{MSD})$ that is averaged over a number of traces indicated on the x-axis. Each point is the average computed from 100 simulations with SD bars. From these simulations, we suggest using at least 20 traces (magenta points) to approximate the diffusion constant and α , but more traces are recommended.

Chapter 2

A paradoxical misperception of relative motion

2.1 Abstract

Detecting the motion of an object relative to a world-fixed frame of reference is an exquisite human capability [Legge, Gordon E., and F. W. Campbell. “Displacement detection in human vision.” *Vision Research* 21.2 (1981): 205-213.]. However, there is a special condition where humans are unable to accurately detect relative motion: Images moving in a direction consistent with retinal slip where the motion is unnaturally amplified can, under some conditions, appear stable [Arathorn, David W., et al. “How the unstable eye sees a stable and moving world.” *Journal of Vision* 13.10 (2013): 22-22]. We asked: Is world-fixed retinal image background content necessary for the visual system to compute the direction of eye motion, and consequently generate stable percepts of images moving with amplified slip? Or, are non-visual cues sufficient? Subjects adjusted the parameters of a stimulus moving in a random trajectory to match the perceived motion of images moving contingent to the retina. Experiments were done with and without retinal image background content. The perceived motion of stimuli moving with amplified retinal slip was suppressed in the presence of a visible background; conversely, higher magnitudes of motion were perceived under conditions when there was no background. Our results demonstrate that the presence of retinal image background content is essential for the visual system to compute its direction of motion. The visual content that might be thought to provide a strong frame of reference to detect amplified retinal slips, instead paradoxically drives the misperception of relative motion.

2.2 Introduction

Detecting relative motion is one of the exquisite sensitivities of human visual perception. Yet, there is a special condition in which humans fail to accurately detect relative motion.

During fixational drift, when the retinal slip of an image is unnaturally amplified, the retinal image appears stable, even in the presence of world-fixed retinal background content that might have served as a frame of reference [5, 70].

This so-called “illusion of relative stability” for all images moving in the direction of retinal slip, regardless of amplitude, suggests that the visual system knows its direction of motion and that anything moving in a direction consistent with the direction of retinal slip, is rendered in the percept to be stable. This is an important extension of the well-known fact that, despite ever-present fixational eye movements which are large enough to make details of the scene sweep across the retina by a detectable amount, the world appears stable. The mechanisms for perceptual visual stabilization are unknown. How is the direction of eye motion determined? Specifically, is world-fixed retinal image background content needed to compute the direction of eye motion or are non-visual cues (e.g. efferent copy) sufficient? Arathorn et al. [5] were unable to answer these questions because they could not adequately control or remove world-fixed retinal content from the visual scene. We have addressed that limitation using an updated system wherein we can fully control or remove retinal image content. We designed a method-of-adjustment experiment to quantify the perceived motion of stimuli moving in different directions with respect to eye motion in conditions with and without retinal image background content.

Our findings indicate that the sensory signals that inform the visual system about its direction of motion are retinal-image based. In conditions with retinal image background content, the perceived magnitude of motion of images moving with amplified retinal slip was significantly lower than that of images moving in the same direction as eye motion. When we performed the same experiments with no visible background – an unusual circumstance in the real world – we found that these perceptions reversed; images with increased retinal slip were perceived to have a high magnitude of motion while images moving in the same direction were perceived as having little to no motion. The retinal background content – that would normally be considered to provide a strong frame of reference for detecting motion – paradoxically drives the misperception of relative motion.

2.3 Results

We measured the perceived motion of stimuli moving with increased retinal slip (Gain -1.5) and moving in the same direction as retinal motion (Gain $+1.5$). The definition of the Gains are shown in Fig. 2.1b. Because the motion of these stimuli is dependent on retinal motion, we call these “retina-contingent stimuli.” The specific Gains were chosen for two reasons: first, because they both generate the same amount of world motion for any given retinal motion and second, because if we chose Gain $+1$ and -1 , the Gain $+1$ condition, being stabilized on the retina, would quickly fade from view and preclude reliable matching. We additionally tested world-fixed stimuli (Gain 0) as a control. Motion perceptions were recorded under two conditions: in the presence of rich retinal image background content (Fig. 2.1d) and with no visual cues (Fig. 2.1e). In this study, we refer to these conditions

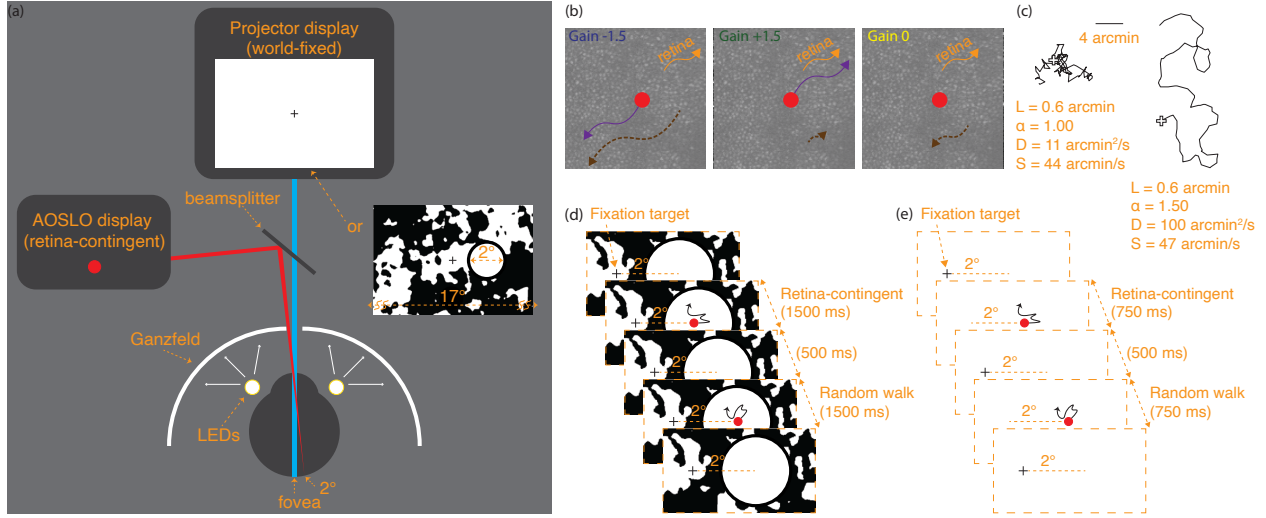


Figure 2.1: Display configuration. (a) The projector drew a fixation target and the surrounding 17° field displayed either white light or a binarized noise pattern. The AOSLO generated the stimuli positioned 2° temporal to the fovea (nasal field). These images were simultaneously projected onto the retina through a beamsplitter. (b) Rules for the three retina-contingent stimuli. Each panel shows an identical retinal trajectory indicated by the orange arrows. The purple arrows indicate the stimulus' trajectory in the world. A Gain -1.5 stimulus moves with increased retinal slip, a Gain $+1.5$ stimulus moves in advance of retinal motion, and a Gain 0 stimulus is world-fixed. The dashed-brown arrows indicate the stimulus' trajectory across the retina. A Gain -1.5 stimulus moves $2.5\times$ more on the retina than a Gain 0 stimulus, and a Gain 0 stimulus moves $2\times$ more on the retina than a Gain $+1.5$ stimulus. (c) Simulated trajectories showing uncorrelated, Brownian motion (left) and positively correlated, persistent motion (right). The white cross indicates the starting position for each trace. Both paths were generated from the same average step length, $L = 0.6$ arcminutes, and have similar speeds (S), yet have different diffusion constants (D) due to different degrees of persistence, indicated by the value α . Full descriptions of these parameters are provided in Chapter 1, Section 1.1. (d-e) Experiment sequence. Subjects fixated on the target and attended to the stimuli positioned 2° temporally. The retina-contingent stimulus moved contingent to each subject's idiosyncratic fixational eye motion. The random walk stimulus moved independent of eye motion, with pre-generated random offsets. Under background-present conditions (d), the projector field displayed a binarized noise pattern which changed after each presentation and the fixation target remained on for the entire duration. Under background-absent conditions (e), a "Ganzfeld effect" was achieved by setting up a white paper with an aperture in front of the display permitting only the AOSLO and projector beams to enter the eye, shown in (a). LEDs were taped around the eye to illuminate the paper and the luminance was adjusted so that the subject saw only the stimuli in a white full-field surround. Owing to its proximity to the eye, the natural blur of the aperture rendered the transition between the display and luminance-matched paper invisible. The fixation target was timed to turn off when the stimuli were presented.

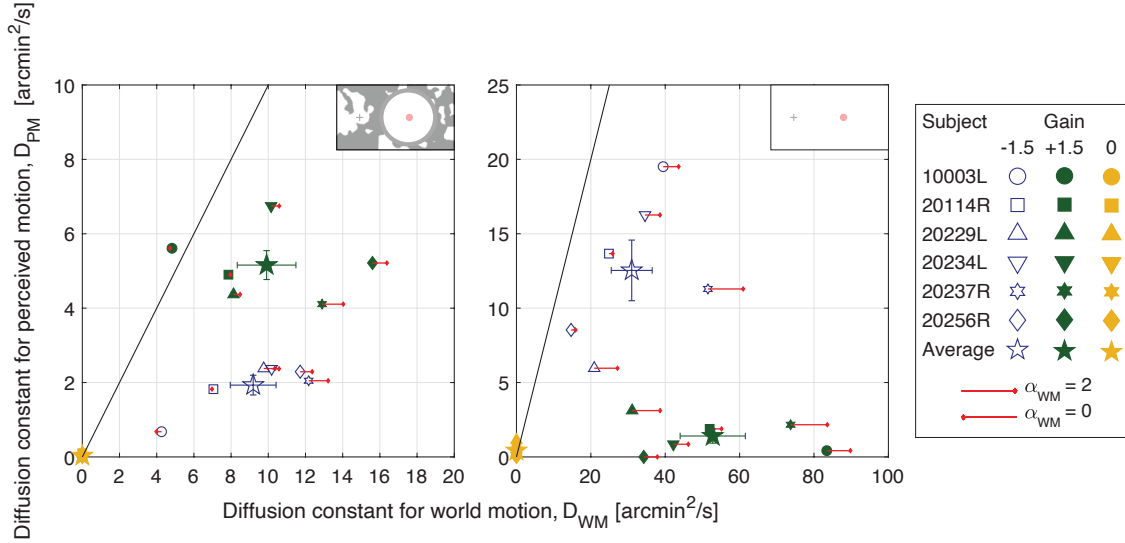


Figure 2.2: Average diffusion constants for perceived motion (D_{PM}) versus diffusion constants for world motion (D_{WM}) from six subjects. Experiments were tested under background-present and background-absent conditions, indicated by labels on the top right corner of each graph. The small symbols represent each subject’s average perceptual match for Gain -1.5 stimuli (blue open symbols), Gain $+1.5$ stimuli (green filled symbols), and Gain 0 stimuli (yellow filled symbols). The large stars are the group averages with standard error of the mean bars. The red arrows show the extent to which the eye motion, and consequent retina-contingent stimulus’ world motion (α_{WM}), deviated from Brownian. Arrows pointing right indicate persistence ($\alpha_{WM} > 1$), arrows pointing left indicate antipersistence ($\alpha_{WM} < 1$), and no arrow means that the motion was Brownian ($\alpha_{WM} = 1 \pm 0.02$). Longer arrows correspond to higher deviations from Brownian motion. The arrow length in the legend indicates pure persistence ($\alpha_{WM} = 2$, straight line trajectory at constant velocity) if pointing right or pure antipersistence ($\alpha_{WM} = 0$, oscillatory motion) if pointing left.

as “background-present” and “background-absent,” respectively.

The experiment ran as follows (full details in Materials and Methods). Subjects simultaneously viewed a world-fixed projector display and a second display, delivered through an adaptive optics scanning light ophthalmoscope or AOSLO (Fig. 2.1a). For each presentation, the subject held their gaze on a projector-generated fixation cross while attending to the motion of an AOSLO-generated circular stimulus presented 2° in the horizontal periphery. The retina-contingent stimulus was presented in the first time interval. Following a 500-ms interstimulus interval, the stimulus in the second interval moved with pre-programmed random walk offsets, independent of eye motion, with a controllable magnitude quantified by its diffusion constant, see Materials and Methods and Equation 1.1.

The subject’s task was to observe the motion in each interval and then adjust the diffusion constant of the stimulus in the second interval (random walk stimulus) until its motion looked

equivalent to that of the stimulus in the first interval (retina-contingent stimulus). No specific criteria were given for making a match and subjects expressed no difficulty or frustration to achieve one. Subjects could view as many self-initiated presentations as they wished for each Gain condition while adjusting the match. They were instructed to view their final match at least three times before submitting. The diffusion constant of the random walk stimulus which the subject submitted as a match in perceived motion (PM) will be called D_{PM} . All the Gain conditions were presented in a pseudorandom order until six matches were submitted for each.

The AOSLO is a custom-built device that can image and track the retina in real time and deliver the retina-contingent stimuli with sub-arcminute accuracy [6]. A description of the system and its schematic are provided in Chapter 1, Section 1.1. An AOSLO video of the retina containing a version of the stimulus embedded as a decrement on each video frame was recorded for each presentation. The videos were analyzed offline to compute the following: a continuous eye motion trace; the trajectory of each retina-contingent stimulus; and the accuracy of the retina-contingent stimulus. We computed the diffusion constant for the eye motion (EM) (D_{EM}) and the diffusion constant for the world motion (WM) of the stimulus (D_{WM}). Also, since the eye does not always exhibit true Brownian motion, we computed a second parameter, α , which quantified the extent to which the eye motion (and consequently the retina-contingent stimulus motion) was either persistent ($\alpha > 1$) or antipersistent ($\alpha < 1$) [22]. Across all traces for each trial, we computed a single D_{WM} and α_{WM} per match, from the average of all valid retina-contingent presentations. Lastly, we computed the average drift speed (S_{EM}). Full descriptions of the motion parameters are in Materials and Methods.

Fig. 2.2 plots the average responses from experiments tested under background-present (left) and background-absent (right) conditions. The retina-contingent stimulus' diffusion constant for perceived motion (D_{PM}) is plotted as a function of its diffusion constant for world motion (D_{WM}). Each small data point represents one subject and is the average of six trials. Refer to Fig. 2.8 for individual subject distributions of the six trials. The large stars represent the group averages with standard error of the mean bars. The data points that lie along the diagonal 1:1 line represent trials where the perceived motion of the retina-contingent stimulus was equivalent to the stimulus' actual motion occurring in the world. The red arrows depict the extent to which the α for the world motion (α_{WM}) deviated from Brownian motion. Arrows pointing right represent persistence ($\alpha_{WM} > 1$), arrows pointing left represent antipersistence ($\alpha_{WM} < 1$), and the absence of an arrow indicates Brownian motion ($\alpha_{WM} = 1 \pm 0.02$). Each red arrow represents the average α_{WM} from six trials, individual trial distributions are shown in Fig. 2.8. We did not show red arrows for the Gain 0 stimuli because the stimuli are world-fixed and motion statistics do not apply.

Comparing Perceived Motion for Gain +1.5 and -1.5.

Under background-present conditions (Fig. 2.2, left), images moving in the same direction as eye motion (Gain +1.5) were perceived to have more motion than images moving with

increased retinal slip (Gain -1.5). This means that despite the Gain -1.5 stimuli having similar world motion, as well as approximately five times more retinal motion than the Gain $+1.5$ stimuli, all subjects reported seeing it as having significantly less motion ($p = 0.0029$, post hoc Tukey-Kramer). This is consistent with the findings of Arathorn et al. [5] for which some world-fixed background content could not be avoided.

Under background-absent conditions (Fig. 2.2, right), the motion perceptions reversed. Images moving with increased retinal slip (Gain -1.5) were now perceived to be moving with a high magnitude of motion whereas subjects reported perceiving little to no motion when images moved in the same direction as eye motion (Gain $+1.5$).

The striking reversal in perceptions shows how profoundly the presence of retinal image background content impacts perceived motion. For Gain -1.5 stimuli, all subjects reported perceiving a higher magnitude of motion under background-absent conditions (average $D_{PM} = 12.54$ arcmin²/s, sem ± 2.04 arcmin²/s) compared to background-present conditions (average $D_{PM} = 1.93$ arcmin²/s, sem ± 0.27 arcmin²/s). Motion perceptions between these conditions were significantly different ($p = 0.0051$, post hoc Tukey-Kramer). For Gain $+1.5$ stimuli, all subjects reported perceiving a lower magnitude of motion under background-absent conditions (average $D_{PM} = 1.41$ arcmin²/s, sem ± 0.48 arcmin²/s) compared to background-present conditions (average $D_{PM} = 5.16$ arcmin²/s, sem ± 0.39 arcmin²/s). Motion perceptions between these conditions were also significantly different ($p = 0.0052$, post hoc Tukey-Kramer).

Ratios Analysis.

To compare the diffusion constant for perceived motion (D_{PM}) and diffusion constant for world motion (D_{WM}) between experiments tested under background-present and background-absent conditions, we computed the ratio $[D_{PM}/D_{WM}]$ for each retina-contingent condition. If subjects always perceived the stimulus' actual motion in the world, then D_{PM}/D_{WM} would be equal to one regardless of background condition. Fig. 2.3 shows the ratios in conditions with background-present plotted on the y-axis and the ratios in conditions with background-absent plotted on the x-axis. The results do not lie on or even close to the 1:1 line – instead the connected data points for each subject show a negative slope, indicative of the reversal of motion perception with background condition.

Perceived Motion for Gain 0.

Under both background-present and background-absent conditions, all subjects reported perceiving little to no motion for world-fixed images (Gain 0) (Fig. 2.2). Under background-present conditions the average $D_{PM} = 0.033$ arcmin²/s, sem ± 0.020 and under background-absent conditions, the average $D_{PM} = 0.43$ arcmin²/s, sem ± 0.18 . Motion perceptions between these conditions were not significantly different ($p = 0.064$, post hoc Tukey-Kramer). The average perceived motion for Gain 0 stimuli were lower than the average perceived motion of Gain -1.5 and Gain $+1.5$ stimuli, with the exception of 20256R, where the subject

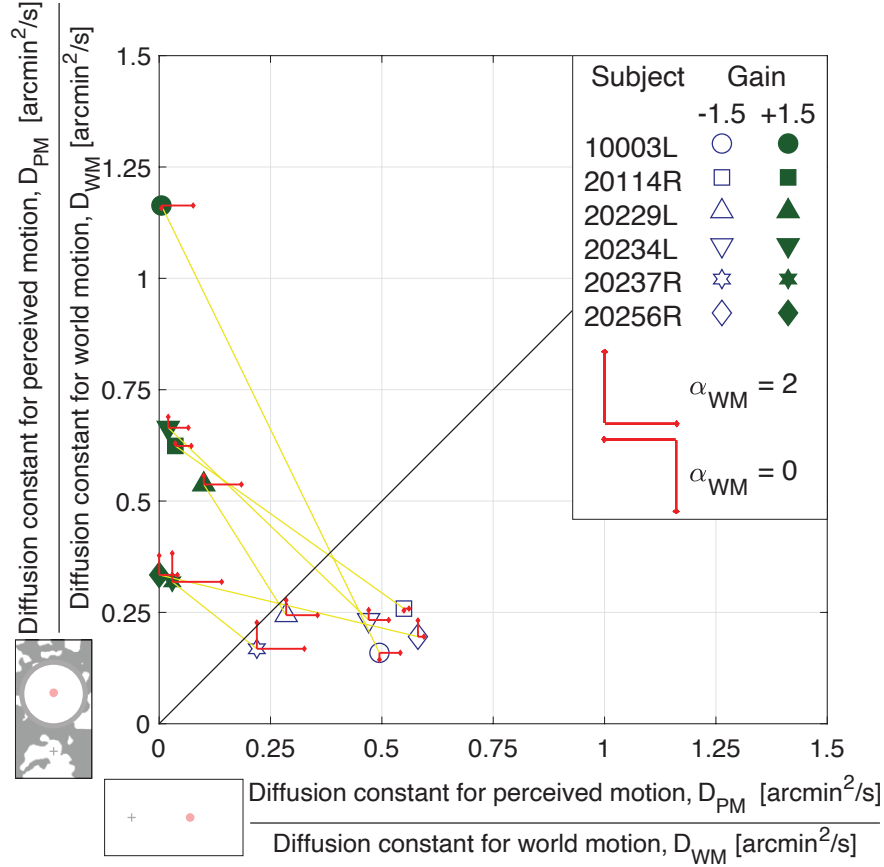


Figure 2.3: Computed ratios from six subjects tested under background-present (y-axis) and background-absent (x-axis) conditions. The symbols represent each subject's [average diffusion constant for perceived motion] / [average diffusion constant for world motion] for two Gain conditions: Gain -1.5 stimuli (blue open symbols) and Gain $+1.5$ stimuli (green filled symbols). The red arrows show the extent to which the eye motion, and consequent retina-contingent stimulus' world motion (α_{WM}), deviated from Brownian. Arrows pointing up and right indicate persistence ($\alpha_{WM} > 1$) under background-present and background-absent conditions, respectively. Arrows pointing down and left indicate antipersistence ($\alpha_{WM} < 1$) under background-present and background-absent conditions, respectively. No arrow means that the motion was Brownian ($\alpha_{WM} = 1 \pm 0.02$). Longer arrows correspond to higher deviations from Brownian motion. The arrow length in the legend indicates pure persistence ($\alpha_{WM} = 2$, straight line trajectory at constant velocity) if pointing up/right or pure antipersistence ($\alpha_{WM} = 0$, oscillatory motion) if pointing down/left.

perceived no motion for both Gain 0 and Gain +1.5 under background-absent conditions (Fig. 2.2, right).

Comparing Perceived Motion for Gain +1.5 and 0 Under Background-Absent Conditions.

Subjects reported seeing little to no motion when viewing the Gains 0 and +1.5 stimuli under background-absent conditions. Motion perceptions were not significantly different between the Gains 0 and +1.5 stimuli ($p = 0.057$, post hoc Tukey-Kramer). The eye motion was not significantly different between Gain +1.5 and Gain 0 presentations, shown in Fig. 2.4a. However, the Gain 0 stimuli moved across the retina with greater retinal motion (RM) than Gain +1.5 stimuli: The average diffusion constant for retinal motion (D_{RM}) of a Gain 0 stimulus was $15.55 \text{ arcmin}^2/\text{s}$, while the average D_{RM} of a Gain +1.5 stimulus was $5.86 \text{ arcmin}^2/\text{s}$ (see Materials and Methods).

Eye Motion Depends on Background and Stimulus Condition.

The diffusion constant for eye motion (D_{EM}), α for eye motion (α_{EM}), and speed for eye motion (S_{EM}) for all Gains and background conditions are plotted on Fig. 2.4.

Under background-present conditions, D_{EM} was not significantly different between Gain conditions (Fig. 2.4a). Most, but not all, eyes exhibited a small degree of persistence ($\alpha_{EM} > 1$) but the α_{EM} did not significantly differ between Gain conditions (Fig. 2.4b). The S_{EM} during Gain -1.5 stimuli presentation was slightly higher than that of the Gain 0 stimuli presentation (Fig. 2.4c).

The D_{EM} and S_{EM} were uniformly greater for all Gains under background-absent conditions, meaning there was more eye motion. While α_{EM} values were greater for all Gains under background-absent conditions, only Gain +1.5 and 0 conditions showed a significant increase.

Under background-absent conditions, the D_{EM} of the Gain +1.5 stimuli was significantly greater than that of the Gain -1.5 . The α_{EM} values were greater than one for all Gain conditions but were greatest for the Gain +1.5 condition.

To offer a physical sense of the differences in α_{EM} values between background conditions, all the gaze trajectory traces during the Gain -1.5 retina-contingent stimulus presentations are plotted for one of the subjects in Fig. 2.5 a and b and for all subjects and all conditions in Fig. 2.9.

The Presence of Persistent Eye Motion ($\alpha_{EM} > 1$) Affects Interpretation of the Results.

Subjects adjusted the diffusion constant of the random walk stimulus until its motion looked perceptually equivalent to the motion of the respective retina-contingent stimulus. Although

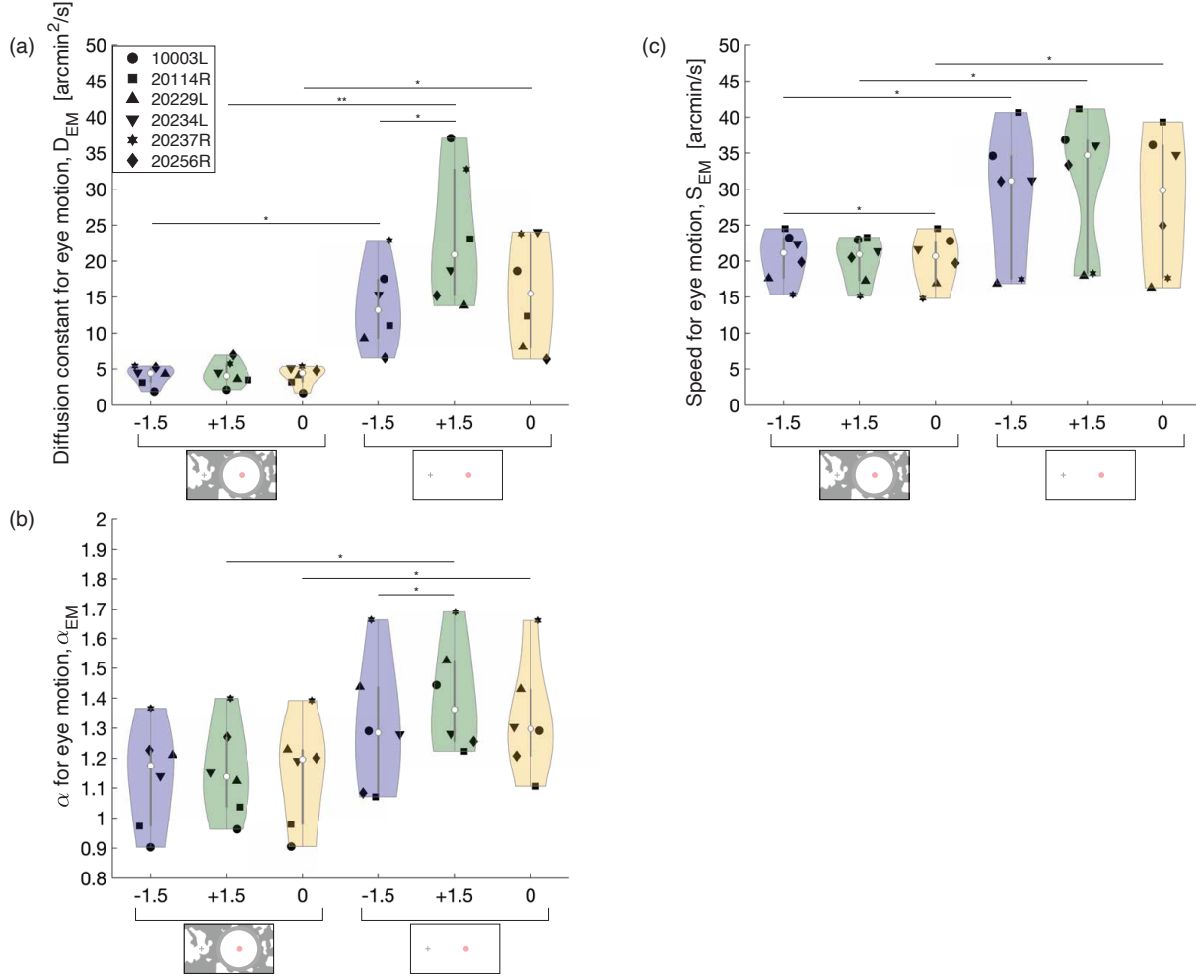


Figure 2.4: **a-c** Violin plots [8] showing the distribution of the (a) diffusion constant for eye motion, D_{EM} , (b) α for eye motion, α_{EM} , and (c) speed for eye motion, S_{EM} , for three Gains (-1.5 , $+1.5$, and 0) under two conditions (background-present and background-absent). In the center of the violins, the white circles and dark bars represent the median and interquartile range, respectively; these are surrounded by the density trace [34]. The black points are the (a) average D_{EM} , (b) average α_{EM} , and (c) average S_{EM} for each subject across their six respective trials for each Gain. The asterisks indicate statistical significance ($p < 0.05$ and $p < 0.01$, respectively) from a post hoc Tukey-Kramer test following a two-factor repeated-measures ANOVA.

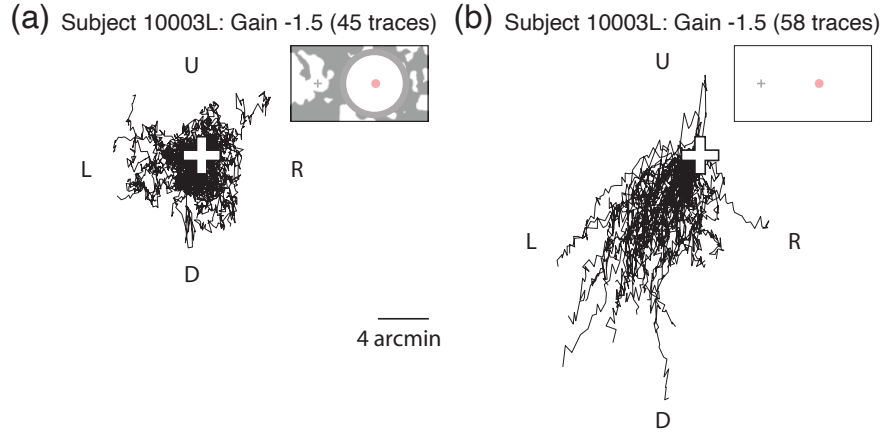


Figure 2.5: Example gaze traces for subject 10003L during Gain -1.5 retina-contingent presentations under (a) background-present (1500-ms duration and $\alpha_{EM} = 0.90$) and (b) background-absent (750-ms duration and $\alpha_{EM} = 1.29$) conditions. The white cross indicates the starting position for each trace. The gaze directions are labeled: left (L), right (R), up (U), and down (D).

Fig. 2.4 shows that α for eye motion (α_{EM}) changed between conditions and was mostly persistent, we chose to constrain the motion of the random walk matching stimulus to be Brownian motion with α , on average, equal to one.

We constrained the motion of the random walk matching stimulus to be Brownian because we found that subjects perform poorly at discriminating a highly persistent motion (e.g. $1.3 < \alpha < 1.7$) with a high diffusion constant from a less persistent motion (e.g. $1 < \alpha < 1.3$) with a low diffusion constant. This was found when we ran a control experiment with the same method-of-adjustment procedure, but with controlled random walk stimuli in both intervals. The stimulus in the first interval was a pre-programmed random walk stimulus with a selected α and diffusion constant. The subject's task was to adjust the parameters of the random walk stimulus in the second interval until its motion looked equivalent to that of the random walk stimulus in the first interval. Subjects could adjust two parameters – the diffusion constant as well as the α . We repeated each match two times. We found that for the same test α and diffusion constant, sometimes the subject would correctly match the α and diffusion constant, while for other matches the α and diffusion constant were both much higher or both much lower (Fig. 2.10). What could contribute to this mismatch, is that random walks with high α and diffusion constant values can be generated from the same average step length as random walks with low α and diffusion constant values, examples are shown in Fig. 2.1c. We concluded that introducing a second adjustable parameter, α , complicated the interpretation of results and also made the experimental procedure more difficult for the subject. We therefore ran experiments with one adjustable parameter, the diffusion constant, and set the α to be on average equal to one.

We could not, however, control the α for the world motion (α_{WM}) of the retina-contingent stimuli because the subjects' fixational eye motion governed this parameter.

When the α_{WM} is different from the α_{PM} , comparing only their diffusion constants is too simplistic. This is because the α and diffusion constant are dependent on each other.

A subject with persistent eye motion, would have a high α_{WM} value and thus a higher diffusion constant, compared to a trajectory with the same average step length but with an α equal to one. This could explain why, in Fig. 2.3, the subjects with high α_{WM} did not report D_{PM} equal to the D_{WM} . The subjects with more persistent motion ($\alpha_{WM} > 1$, larger red arrows) tended to have lower ratio values. These higher α_{WM} values correspond to higher D_{WM} which increase the value in the denominator.

Fig. 2.6 plots the ratios from Fig. 2.3 as a function of each subject's α_{WM} , for two of the conditions: Gain -1.5 stimuli tested under background-absent conditions and Gain $+1.5$ stimuli tested under background-present conditions. To predict how the presence of persistent eye motion could impact the interpretation of the results, we modeled how the ratio of the diffusion constants would vary with α_{WM} under a specific condition where the subject equated the mean square displacement (MSD) between the motion of the retina-contingent stimulus and the motion of the random walk stimulus over a time interval (ΔT) of 2 frames. In the model, the random walk stimulus' α , which represents the α for perceived motion (α_{PM}), is equal to one (Brownian motion) and the retina-contingent stimulus' α_{WM} ranges from antipersistent ($0.9 \leq \alpha_{WM} < 1$), to Brownian ($\alpha_{WM} = 1$), to persistent ($1 < \alpha_{WM} \leq 1.8$). The model is represented by the solid curve in Fig. 2.6. The derivation and full descriptions of these parameters are in Materials and Methods.

As the retina-contingent stimulus' α_{WM} becomes more persistent, it on average traverses further than a Brownian stimulus and therefore the mean square displacement of the trajectory increases faster over a time interval compared to that of the Brownian stimulus.

The model shows that there is an exponential decay relationship between D_{PM}/D_{WM} and α_{WM} – as the eye motion becomes more persistent ($\alpha_{WM} > 1$), the corresponding D_{WM} increases and subsequently the ratio D_{PM}/D_{WM} decreases. The human subject data are largely predicted by this model.

2.4 Discussion

When an object moves in the world, the image that is cast onto the retina has retinal motion both due to the object's motion as well as the fixational eye motion. To properly perceive an object's motion in the world, the visual system is tasked with disentangling the two [31, 57]. Normally, the visual system performs this task exceptionally well; humans are able to reliably perceive world-fixed objects as stable and can identify moving objects within it with hyperacuity [42, 88]. Yet, in conditions where an image is programmed to move with amplified retinal slip, humans exhibit a paradoxical inability to accurately perceive the motion of the image relative to a high-contrast, world-fixed background.

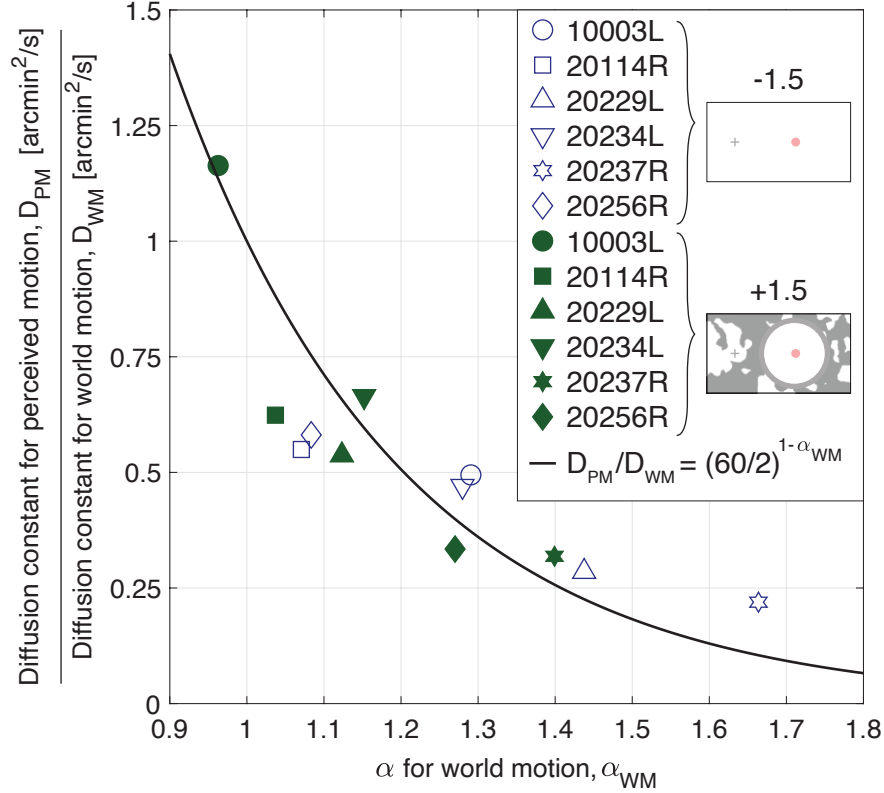


Figure 2.6: Computed ratios from six subjects plotted as a function of each subject's α for world motion, α_{WM} . The symbols represent each subject's [average diffusion constant for perceived motion] / [average diffusion constant for world motion]. Data from two experiments are shown: Gain -1.5 stimuli tested under background-absent conditions (blue open symbols) and Gain $+1.5$ stimuli tested under background-present conditions (green filled symbols). The black curve predicts the D_{PM}/D_{WM} versus α_{WM} , considering that the subject matched the mean square displacements of the random walk stimulus with the retina contingent stimulus over a time interval of 2 frames. Because the random walk stimulus motion is Brownian ($\alpha_{PM} = 1$) and the retina-contingent stimulus' motion ranges from antipersistent ($0.9 \leq \alpha_{WM} < 1$), to Brownian ($\alpha_{WM} = 1$), to persistent ($1 < \alpha_{WM} \leq 1.8$) the curve shows an exponential decay, which largely matches the data.

Our findings support those of Arathorn et al. [5] and demonstrate that the visual system suppresses the perceived motion of anything moving in a direction consistent with retinal slip (Gains less than 1), despite their magnitude. The neural mechanism for doing this has yet to be described but from a vision standpoint it is functionally sufficient, since the likelihood that any real-world object would be moving in the same direction of retinal slip for any appreciable duration is effectively zero. All other directions, such as our Gain +1.5 and all other Gain conditions described in Arathorn et al. [5], are perceived as moving. As a control, we tested the same experiment for one subject, presenting a stimulus that moved with a Gain of +1.5, but programmed to move orthogonal to eye motion. There was no significant difference in motion perception between this stimulus and the stimulus that moved in advance of eye motion, Gain +1.5 (Fig. 2.11).

This chapter shows that the direction of eye motion must arise from the retinal image content itself (inflow) and is not relayed to the visual system by any other non-visual means, such as efference copy.

To further understand the process, we first review what is known functionally and structurally about perception of motion.

Perceiving the World As Stable.

Previous studies showed that the retinal input informs the visual system about image motion on the retina due to drift. Poletti et al. [63] presented gaze-contingent stimuli using a dual Purkinje eye tracker in conditions with and without frames of reference. Consistent with our findings on Fig. 2.2, stimuli moving in the same direction as gaze (there was a Gain +1 condition, which meant the image was stabilized) were perceived to move when frames of reference were present, and perceived as stable when all visual content was removed. They concluded that the retinal input drives the compensation of retinal motion.

A possible origin of the retinal signal is directionally sensitive retinal ganglion cells (DSRGCs) for which evidence of their existence in primate and human retina continues to mount [85, 61, 38]. The subclass of ON-OFF DSRGCs, which project to the LGN and subsequently the visual areas of the cortex, are the most likely candidates. Combined signals from a sufficient number of these cells to eliminate ambiguity could be used to compute the direction of retinal slip, which may provide partial information to the downstream circuitry to assist in the stabilization process. Exactly how and where the stabilization occurs however, is not known and evidence is mixed [3, 32, 53, 48].

Detecting Moving Objects.

Humans have a hyperacute ability to detect [49] and resolve [42] the motion of objects within a visual scene. The neural underpinning for detection of these stimuli in the presence of incessant eye movements may lie in the Object Motion Sensing (OMS) ganglion cells. Yet to be found in primates, this class of retinal ganglion cells is very effective at identifying an object that is moving differently than the surround [57].

But despite increasing knowledge of the neural systems that underlie our ability to perceive a stable and moving world [37], what remains unclear is how two objects that move in a direction consistent with retinal slip but with different velocities can be rendered in the percept to be fixed relative to each other.

The Role of Efference Copy.

Studies have shown that efference copy or other non-visual cues can inform the visual system about its gaze direction during drift [66, 90], albeit not with great accuracy. In our experiments, however, it is very clear from the background-absent condition that neither efference copy nor any other nonvisual signal is being used effectively to determine the direction of motion in a manner that guides perception of moving objects. That being said, the perception of motion in the background-absent condition cannot be explained as being due simply to retinal motion either. For example, the Gain 0 condition, which actually moved more across the retina than the Gain +1.5 condition, was perceived to be moving either the same (subject 20256R), or less than the Gain +1.5 condition. Further investigations of this condition are warranted.

Precedence in Prior Literature.

The level of stimulus control in this study is unprecedented so, aside from an earlier study by coauthors of the current paper [5] and a brief mention in the early stabilization literature [70], there is no other study that is directly comparable. However, some level of control of the retinal slip can be accomplished during a smooth pursuit task. In the most relevant study, Turano and Heidenreich [83] explored the detectability of changes in the motion of sinusoidal grating while the subject pursued a simultaneously presented smooth pursuit stimulus that moved faster or slower than the grating. When the smooth pursuit stimulus moved slower than the grating, the subject exhibited an expected sensitivity to differences in grating motion. However, when the smooth pursuit target moved faster than the grating, subjects exhibited an unexpected difficulty detecting changes in grating motion. This second condition is similar in a way to our own in that their grating, on average, slipped in a direction consistent with retinal motion, but with a different magnitude than the surround. So, while the authors were unable to explain these phenomena, they are not surprising or unexpected in the context of our results.

Another field of study involves the perception of motion using widely studied stimuli like those that give rise to the Ouchi illusion [58] and the related jitter after-effect [55]. This class of experiment provides strong evidence that retinal image content provides important cues to eye motion. Interestingly, our study explores the inability to perceive relative motion where it does exist, while this other class of studies explore the opposite: perceived relative motion where it does not exist. Nevertheless, these are complementary to each other.

Control Experiments to Validate Results.

In this study, we presented stimuli for 1500-ms under background-present conditions and for 750-ms under background-absent conditions. These duration choices were motivated by a trade-off to achieve robust motion judgements while also optimizing retinal tracking. A longer interval duration gives the subject sufficient time to discern the motion magnitude of the stimuli but can also lead to tracking failures if the eye drifts too far away from fixation. We performed control experiments on subjects 10003L and 20114R to verify that different stimulus durations did not contribute to the results. We presented the stimuli for 750-ms intervals under background-present conditions and found similar trends, although less robust, as experiments with 1500-ms intervals (Fig. 2.12). Under background-absent conditions, the eye had faster drift and larger corrective microsaccades which led to tracking failures and as a result, we were unable to perform the experiments with 1500-ms stimulus intervals.

In the experiments tested under background-absent conditions, we ensured no frames of reference were visible to the subject, even removing the fixation target during the retina-contingent interval and the random walk interval. Under these conditions, we could not truly assess the amount of motion perceived. Specifically, we could not conclude that the subject did not perceive motion when they matched a Gain 0 condition to a non-moving stimulus in the second interval. As a check, we performed a control experiment for one subject with the same experimental protocol, except that the fixation target remained on to serve as a frame of reference during the random walk interval. We found no difference in matches to the Gain 0 stimuli whether the fixation target was on or off during the random walk interval (Fig. 2.13).

Summary.

This study employs a powerful combination of high resolution retina tracking with stimulus delivery to reveal striking properties of absolute and relative motion perception that would otherwise not have been discovered in natural viewing conditions. The retinal-image-based signals that the visual system uses to generate a stable percept of the world are so potent that they can disrupt our fundamental skill of detecting relative motion. This dichotomy suggests that evolution settled on a mechanism that optimized behavior in the majority and most critical visual circumstances, and tolerated anomalous behavior in outlier observing conditions. The knowledge provided has crucial implications for those who aim to elucidate the neural underpinnings of this important property of human vision.

2.5 Methods

Subjects.

Six subjects (4 experienced and 2 naive) were recruited. The experiment was approved by the Institutional Review Board at the University of California, Berkeley. Prior to the

experiment, subjects provided informed consent to participate. We applied topical eye drops of 1.0% tropicamide and 2.5% phenylephrine hydrochloride to dilate and cycloplege subjects prior to each experiment.

Adaptive Optics Scanning Light Ophthalmoscopy.

Retinal imaging and stimulus delivery were performed using a multiwavelength AOSLO [54, 74]. Refer to Chapter 1, Section 1.1, for a full description of the system and its capability to perform real-time eye tracking.

Projector Display.

A DLP LightCrafter projector (DLP4500; Texas Instruments, Dallas, TX, USA) displayed a 17° background which projected over the 840-nm imaging raster. The mean luminance of the display, which was approximately 540 cd/m^2 , effectively canceled perception of the 840- and 940-nm rasters. A fixation target and patterns were drawn over the background and timed with the stimulus delivery dependent on the experiment conditions (Fig. 2.1 d and e). The procedure was programmed with MATLAB (MathWorks, Natick, MA, USA) using the Psychophysics Toolbox [11, 39, 62].

Retina-Contingent Conditions.

The high-resolution, real-time eye tracking of the AOSLO allowed us to deliver stimuli that moved contingent to fixational eye motion transformed by a “Gain.” The sign of the Gain indicates the direction the image moved with respect to the eye, and the stimulus’ world displacement was equal to the Gain magnitude times the eye displacement. We tested three Gains: -1.5 , $+1.5$, and 0 . The Gain -1.5 stimulus moved directly opposite the direction of eye motion with a magnitude that was 1.5 times that of the eye motion. For example, if the eye moved $2'$ right, then the stimulus moved in the world $3'$ left, producing a total retinal displacement of $5'$. Therefore, in this condition, the stimulus moved on the retina with 2.5 times more motion than a natural, world-fixed object. The Gain $+1.5$ stimulus moved in the same direction as the eye with a magnitude equal to 1.5 times that of the eye motion. For example, if the eye moved $2'$ right, then the stimulus moved in the world $3'$ right. The stimulus moved in advance of eye motion with retinal image motion that was half the retinal motion of a natural, world-fixed object. The Gain 0 stimulus did not move in the world, which means that this was a natural, world-fixed stimulus and served as control.

Generating Random Walks.

Prior to the experiment, we pre-programmed 100s of 750-ms and 1500-ms duration random walks with varying diffusion constants for the subjects to use in the matching task. These paths were generated by computing randomized step lengths in x and y drawn from a normal

distribution with a range of standard deviations from 0.05 to 1.6 arcminutes per step (or AOSLO frame), in increments of 0.05 arcminutes. For the sake of brevity, we will refer to the standard deviation of the randomized step lengths as simply *step lengths* throughout the manuscript. This process effectively randomized the length and direction of each step and, because all directions were equally probable, the α of the paths was approximately equal to one. However, owing to the random nature of generating paths in this method, the same randomized step length could generate paths with a range of possible diffusion constants. We computed the average diffusion constant for each step length, by inputting the step length as the ΔX and ΔY in the mean square displacement formula in Equation 1.2. After solving for the mean square displacement, we input this value into Equation 1.1 to solve for the diffusion constant. For example, a step length of 1.6 arcminutes corresponds to a diffusion constant of 76.8 arcmin²/s. Therefore, for each of the 32 step lengths, we generated 100 paths and from these, we selected the 10 paths with diffusion constants closest to the respective average diffusion constant.

Experimental Design.

Set Up.

The subject's pupil was aligned with the AOSLO beam and their head was immobilized by the use of a dental bite bar.

Conditions.

We tested two conditions. Under the background-present condition, the 17° projector background was filled with rich retinal image background content: a blurred and binarized 1/f noise pattern that changed after every presentation (Fig. 2.1d). The fixation target was present for the entire duration and each stimulus was presented for 1500-ms. Under the background-absent condition, all visual cues were removed (Fig. 2.1e). This was achieved by attaching a white paper with a small central aperture directly in front of the subject, shown in Fig. 2.7. The aperture permitted only the raster and projector light to pass into the subject's eye. The proximity of the aperture to the subject's eye (about 5 cm) ensured that its edges appeared out-of-focus and blurred and therefore blended with the projector view. We then taped LEDs around the subject's eye and the subject adjusted the power of the LEDs until the white projector light was indistinguishable from the paper. Additionally, the fixation target disappeared during the intervals with stimulus presentation. Without a fixation target, eyes generally exhibit faster drift and larger corrective microsaccades [13]. To mitigate the effects of this increased retinal motion on the tracking accuracy, each stimulus was presented for 750-ms.

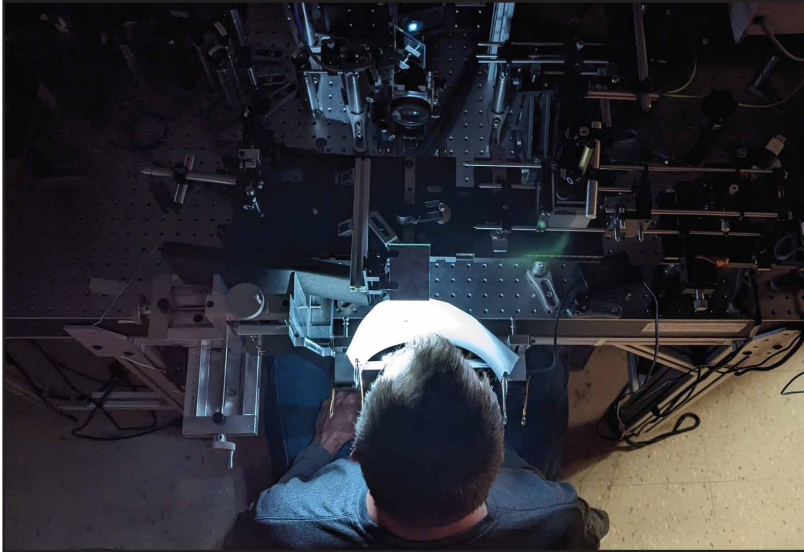


Figure 2.7: Configuration used to generate background-absent conditions. A white paper with a small central aperture was placed directly in front of the subject. The aperture permitted only the raster and projector light to pass into the subject’s eye. The proximity of the aperture to the subject’s eye (about 5 cm) ensured that its edges appeared out-of-focus and blurred and therefore blended with the projector view. We then taped LEDs around the subject’s eye and the subject adjusted the power of the LEDs until the white projector light was indistinguishable from the paper. In this way, all visual cues were removed and subjects perceptually experienced a “Ganzfeld” effect.

Task.

The projector display drew a fixation target positioned 2° nasally away from the AOSLO raster, which remained stationary Fig. 2.1 d and e. The 680-nm light from the AOSLO delivered increment circular images onto the retina, which subtended 12 minutes of visual angle. We tested one retina-contingent condition per trial, either Gain -1.5 , $+1.5$, or 0 . In each trial, the subject could initiate as many presentations as necessary. In a single presentation, the subject attended to the stimulus in the first time interval (retina-contingent), followed by a 500-ms break, followed by the stimulus in the second time interval (random walk). The subject’s task was to adjust the diffusion constant of the random walk stimulus until its motion looked perceptually equivalent to the respective retina-contingent stimulus. When the subject found a match, they initiated a minimum of three final presentations and then submitted their response. In one block, there were six trials and the trial order was randomized. Subjects completed three blocks per background condition. Therefore, for each background condition, there were six trials tested for each Gain. All perceptual responses were made on a gamepad.

Quality Control.

During the experiment, if the subject looked away from the fixation target, the tracking would fail and the stimulus would not be delivered. This ensured that the subject maintained fixation when making motion judgements. Blinks and large saccades also led to tracking failures and the stimulus misdelivery was usually recognizable to the subjects, who were informed ahead of the experiment to disregard presentations with poor stimulus delivery.

After the experiments, we used custom software [2] to extract a continuous eye motion trace from each recorded video. We then used a video-analysis script to determine the retinal positions of the 3 x 3 arcminute stimulus-tracking decrement in each frame. We compared the eye motion trace to the stimulus motion trace to verify that the stimulus moved appropriately contingent to the retina, dependent on the Gain. In this way, videos were evaluated for tracking errors and stimulus misdelivery.

We determined the number of videos where the stimulus delivery was poor but might not have been recognizable to the subject. This was achieved by comparing the eye position to the stimulus-tracking decrement position in frames with retina-contingent presentation. We computed the standard deviation of the stimulus delivery accuracy for each video across all the frames that had retina-contingent stimulus presentation. We considered a video to have poor stimulus delivery when the standard deviation of the stimulus misdelivery from the targeted location was greater than 0.9 arcminutes. If the majority of the videos used by the subject had standard deviations greater than this threshold, we removed the trial. This strict criterion ensured that the motion judgements were not contaminated by presentations with poor tracking. This was especially important for the Gain -1.5 stimuli because tracking errors could cause stimuli motions that no longer slipped in directions consistent with retinal motion, thus disrupting the “illusion of relative stability.”

Because we are interested in motion perception during periods of fixational drift, we used a final filter that removed traces with microsaccades. Microsaccades are linear and ballistic and this would have biased the random walk analysis.

Analysis of Eye Motion and Retina-Contingent Stimulus Motion.

Random Walk Analysis.

Across all traces from each analysis, we quantified the amount of motion (diffusion constant) and its deviation from Brownian motion (α). We performed this random walk analysis on the random walk stimulus’ motion (D_{PM} and α_{PM} , where PM denotes perceived motion), the retina-contingent stimulus’ motion (D_{WM} and α_{WM} , where WM denotes world motion), and the eye’s motion (D_{EM} and α_{EM} , where EM denotes eye motion). Chapter 1, Section 1.1, describes the methods and equations for the statistical analyses we performed to evaluate the random walk motion.

Speed Analysis.

Across all traces with retina-contingent stimulus presentation, we computed the average displacement of the eye over time to compute the speed (S_{EM}). Eye positions were sampled at 60 Hz.

Statistics.

We performed a two-factor repeated-measures analysis of variance (ANOVA) of the alpha for eye motion (α_{EM}), diffusion constant for eye motion (D_{EM}), diffusion constant for perceived motion (D_{PM}), and speed for eye motion (S_{EM}). There were two background conditions (background-present and background-absent) and three retina-contingent stimuli (Gain -1.5 , Gain $+1.5$, and Gain 0), which were within-subject factors. Following the repeated-measures ANOVA, we performed a post hoc Tukey-Kramer test to measure the significance of the pairwise comparisons. We compared between Gain categories within the same background condition and for each Gain we compared differences between background conditions.

Comparing the Eye's Motion and the Retina-Contingent Stimuli's World Motion.

The diffusion constant for world motion (D_{WM}) and α for world motion (α_{WM}) describe how the retina-contingent stimuli move in the world. For the Gain 0 stimulus, D_{WM} is equal to zero because the stimulus is not moving in the world and α_{WM} does not apply. The world motion of the Gains -1.5 and $+1.5$ stimuli are dependent on the parameters of the eye's motion: D_{EM} and α_{EM} . How the eye moves (α_{EM}) is equal to how the non-zero retina-contingent stimuli move (α_{WM}) in the world. However, the eye's magnitude of motion (D_{EM}) is different from the retina-contingent stimulus' magnitude of motion (D_{WM}) because the retina contingent stimulus' motion is transformed by a Gain. There is a squared relationship between the diffusion constant and mean square displacement, therefore, for the Gains -1.5 and $+1.5$ stimuli, the $[D_{WM}] = [D_{EM}] * (1.5)^2$.

Comparing the Eye's Motion and the Retina-Contingent Stimuli's Retinal Motion.

The diffusion constant for retinal motion (D_{RM}) and α for retinal motion (α_{RM}) describe how the retina-contingent stimuli move across the retina. For the Gain 0 stimulus, D_{RM} and α_{RM} are equal to D_{EM} and α_{EM} , respectively, because all retinal motion is the result of the stimulus slipping consistent to the fixational eye motion. The retinal motion of the Gains $+1.5$ and -1.5 stimuli are dependent on the parameters of the eye's motion: D_{EM} and α_{EM} . How the eye moves (α_{EM}) is equal to how the non-zero retina-contingent stimuli move (α_{RM}) on the retina. However, similar to the above paragraph the D_{EM} is not equal to the D_{RM} . The Gain -1.5 stimulus slips with 2.5 times more motion than the eye. The

Gain +1.5 stimulus moves ahead of eye motion and moves with half the motion of the eye. Therefore, for the Gain -1.5 stimuli, the $[D_{RM}] = [D_{EM}] * (2.5)^2$; and for the Gain +1.5 stimuli, the $[D_{RM}] = [D_{EM}] * (0.5)^2$.

Simulated Ratios.

The black curve in Fig. 2.6 models the ratio values versus α for world motion (α_{WM}), where the random walk stimulus' α , which represents the α for perceived motion (α_{PM}), is equal to one (Brownian motion) while the retina-contingent stimulus' α_{WM} ranges from antipersistent ($0.9 \leq \alpha_{WM} < 1$), to Brownian ($\alpha_{WM} = 1$), to persistent ($1 < \alpha_{WM} \leq 1.8$). This model shows how the ratio of the diffusion constants would vary with α_{WM} under a specific condition where the subject equated the mean square displacement (MSD) between the motion of the retina-contingent stimulus and the motion of the random walk stimulus with a specific time interval (ΔT). We tested a range of time intervals and determined by a least-squares procedure that a time interval of 2 frames best predicted the measured data. The units of the time interval are converted to seconds because the AOSLO has a 60 Hz frame rate. Equations 2.1 & 2.2 show the derivation, where the random walk stimulus' motion is represented as the "perceived motion (PM)" and the retina-contingent stimulus' motion is represented as the "world motion (WM)". As the retina contingent stimulus' motion becomes more persistent ($\alpha_{WM} > 1$), the ΔT over which the stimulus reaches higher MSDs becomes smaller compared to the Brownian random walk stimulus. The model assumes that there are no directional biases.

$$D_{PM} = \frac{MSD}{2d\Delta T^{\alpha_{PM}}} \quad D_{WM} = \frac{MSD}{2d\Delta T^{\alpha_{WM}}} \quad (2.1)$$

$$\frac{D_{PM}}{D_{WM}} = \frac{(2/60)^{\alpha_{WM}}}{(2/60)^1} = (60/2)^{1-\alpha_{WM}} \quad (2.2)$$

Data and Code Availability.

Data (CSV files) and Matlab code for all experiments and supplementary information are available at <https://zenodo.org/records/14026507>.

2.6 Appendix 1: Individual Distributions

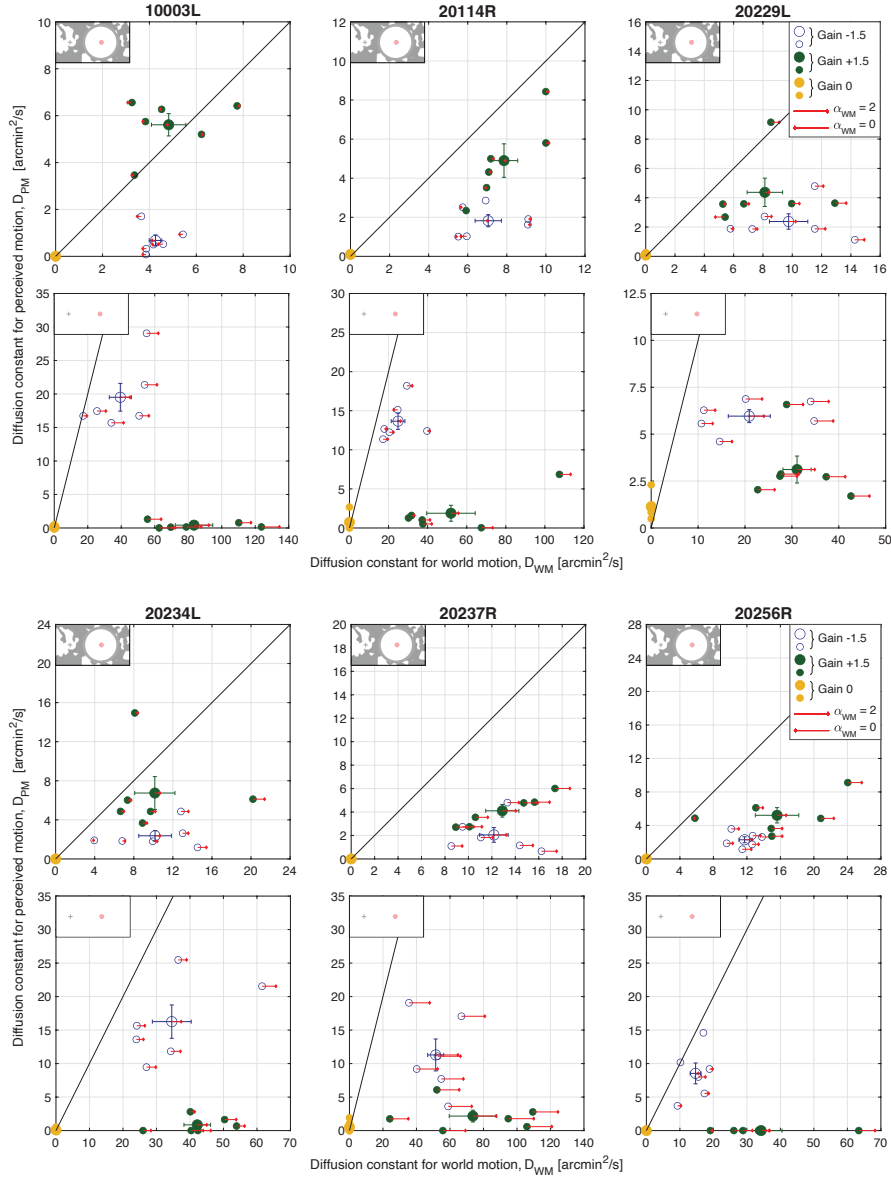


Figure 2.8: Individual results from six subjects tested under background-present and -absent conditions, indicated by labels on the top left corner of each graph. The small circles are the six perceptual matches for Gain -1.5 stimuli (blue open symbols), Gain $+1.5$ stimuli (green filled symbols), and Gain 0 stimuli (yellow filled symbols). The large circles are the averages of the matches with standard error of the mean bars. The red arrows show the extent to which the eye motion, and consequent retina-contingent stimulus' world motion (α_{WM}), deviated from Brownian. Arrows pointing right indicate persistence ($\alpha_{WM} > 1$), arrows pointing left indicate antipersistence ($\alpha_{WM} < 1$), and no arrow means that the motion was Brownian ($\alpha_{WM} = 1 \pm 0.02$). Longer arrows correspond to higher deviations from Brownian motion. The arrow length in the legend indicates pure persistence ($\alpha_{WM} = 2$, straight line trajectory at constant velocity) if pointing right or pure antipersistence ($\alpha_{WM} = 0$, oscillatory motion) if pointing left.

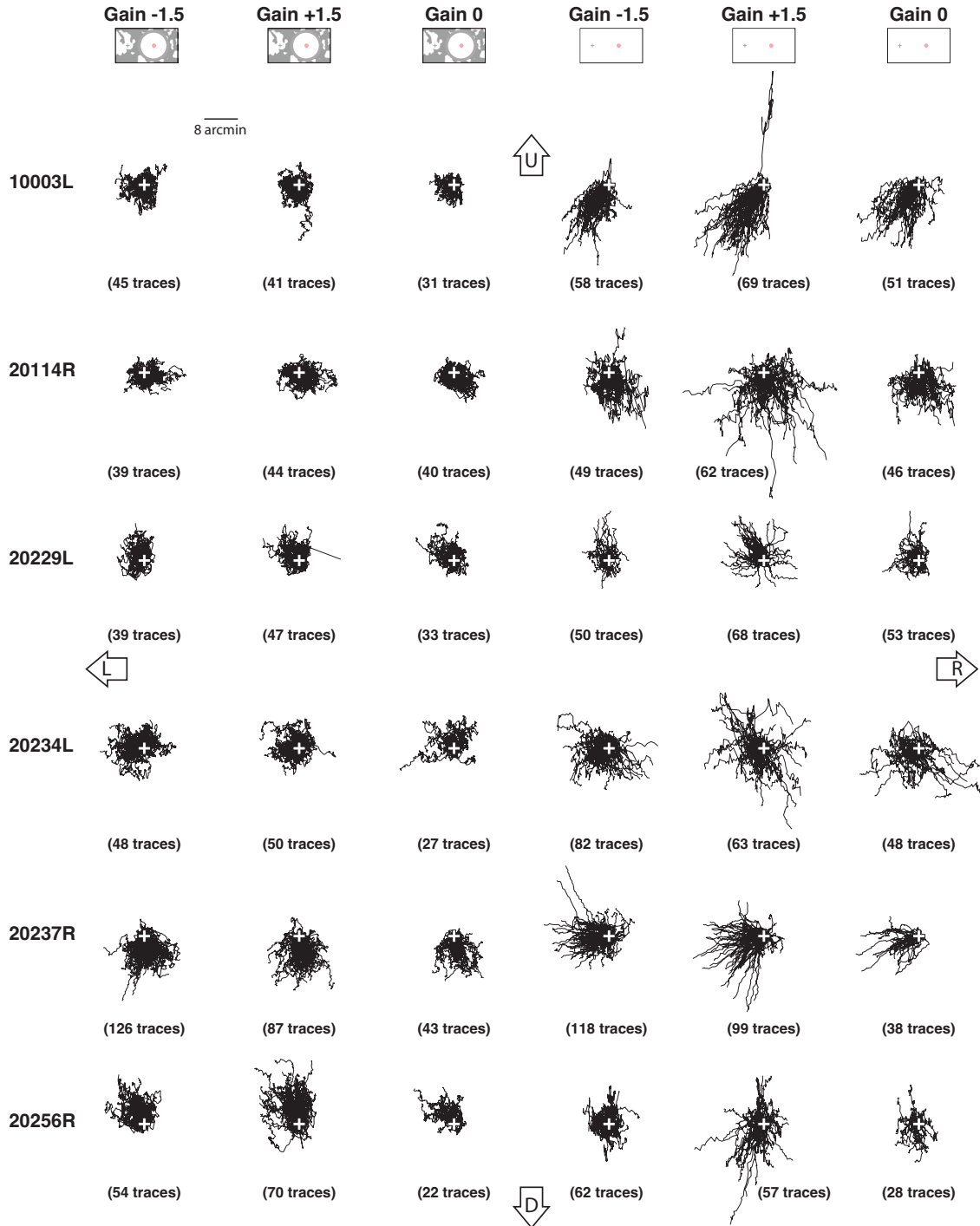


Figure 2.9: Gaze traces for six subjects for the three Gain conditions (-1.5 , $+1.5$, and 0) under background-present (1500-ms duration) and background-absent (750-ms duration) conditions. The Gains and background conditions are indicated by labels at the top of the figure. The white cross indicates the starting position for each trace. The gaze directions are labeled: left (L), right (R), up (U), and down (D).

2.7 Appendix 2: Description of Retina-contingent Stimulus Delivery

This section explains the mechanics of how retina-contingent stimuli are projected onto the retina within the raster-scan of the AOSLO. Note that the raster-scan is always world-fixed so motion of a stimulus in the raster is equivalent to motion in the world.

Definitions.

- Gain: the amplitude of the motion of the projected stimulus relative to the eye motion.
- Angle: the angle of the motion of the projected stimulus relative to the eye motion.

Examples.

- Gain 1 and Angle 0 defines a stabilized stimulus on the retina. The stimulus moves in the raster by an amount that is identical to the eye motion.
- Gain 1 and Angle 180 defines a stimulus that moves in the raster by an amount that is identical to the eye motion, but in the opposite direction. It moves with double the retinal slip across the retina. For simplicity, this is stated in the main manuscript as $\text{Gain} = -1$.
- Gain 1 and Angle 90 defines a stimulus that moves in the raster by an amount that is identical to the eye motion, but rotated by 90° .

For a Raster-Scanned Stimulus Whose Location is Retina-Contingent, the Process is Done in the Following Way.

There is an FPGA board installed in the system computer whose inputs are image data from the AOSLO and whose outputs drive the acousto-optic laser modulators that project the stimulus onto the retina. There is a memory buffer in the FPGA that stores the acousto-optic modulator playout signal that encodes the stimulus. The memory buffer is stored as a 2-D array representing a complete image frame. (NOTE: On the system computer, the stimulus and its location are represented in linear spatial coordinates but there is a transformation between this and the playout memory buffer on the FPGA that accounts for the non-linear sinusoidal scanning of the resonant (fast) scanner. The transformation is done through a lookup table that is generated with a system calibration prior to the experiment.) A reference frame is established prior to initiation and delivery of a retina-contingent display. A stimulus location is identified within the reference frame. This location is set by either a mouse/cursor click or programmed to have a predetermined coordinate (e.g. pixel location 256, 128). The stimulus (e.g. letter 'E') is initially placed in the playout buffer at this raster location. The AOSLO image data is retrieved from the FPGA board in the form of image

strips that comprise the full width of the image and a predetermined height. Typically, in 30 Hz mode the strip height is 16 pixels and there are 32 strips per 512 x 512 frame. In 60 Hz mode, the strip height is 16 pixels and there are 16 strips per frame. The location of each strip is found relative to the reference frame and the ΔX and ΔY offsets required for best registration indicate the new position of the retina relative to the reference frame. The ΔX , ΔY , Gain, & Angle are used to compute the new position of the stimulus. For example, for [Gain = 1, Angle = 90] if the eye has been found to be shifted to the right by 5 pixels (~ 1 arcminute) relative to the reference frame, then the new position of the stimulus in the playout buffer should be up in the raster by 5 pixels. If in the next frame the eye has been found to be shifted to the right by 10 pixels relative to the reference frame, then the new position of the stimulus in the playout buffer is moved up in the raster by 10 pixels. This recomputing of the stimulus position in the playout buffer is done for each strip but the stimulus location in the memory buffer is only updated once per frame when it is determined that the target location will soon be swept by the scanning raster. This once-per-frame update is done to overcome bandwidth limitations (minimize bottlenecks) of data transfer between the CPU and the FPGA. This is OK, since the stimulus in the buffer will not be played out until the raster scans over the location, which also occurs just once per frame. Due to the high-speed processing, the updates of stimulus position are generally made just 2-3 milliseconds prior to the raster passing over the target. It is this low latency that gives the AOSLO its impressive targeting accuracy.

2.8 Appendix 3: Control Experiments

Method of adjustment with two parameters to adjust

To explore the accuracy with which a subject matches two motion trajectories, we performed a method of adjustment experiment with two adjustable parameters: the α and the diffusion constant. The experiment ran as follows, the subject fixated on a fixation target and attended to two stimuli presented over intervals in time. Both stimuli moved on pre-programmed random trajectories, independent to eye motion. The stimulus in the first interval moved with a selected α and diffusion constant. The subject's task was to adjust the α and diffusion constant of the stimulus in the second interval until its motion looked perceptually equivalent to that of the stimulus in the first interval. The subject made their adjustments on a gamepad. Increasing the α parameter greater than one led to more persistent trajectories while decreasing less than one led to more antipersistent trajectories. The α parameter set to one displayed pure random trajectories. Increasing the diffusion constant led to longer path lengths and decreasing the diffusion constant led to shorter path lengths. We tested seven α and diffusion constant combinations: 0.7 and 3.2 arcmin²/s, 0.9 and 1.8 arcmin²/s, 1.0 and 4.8 arcmin²/s, 1.0 and 14.7 arcmin²/s, 1.2 and 24.5 arcmin²/s, 1.5 and 58.1 arcmin²/s, and 1.7 and 84.3 arcmin²/s. We repeated each match two times.

Fig. 2.10 plots the random walks' diffusion constants as a function of the α 's. The seven

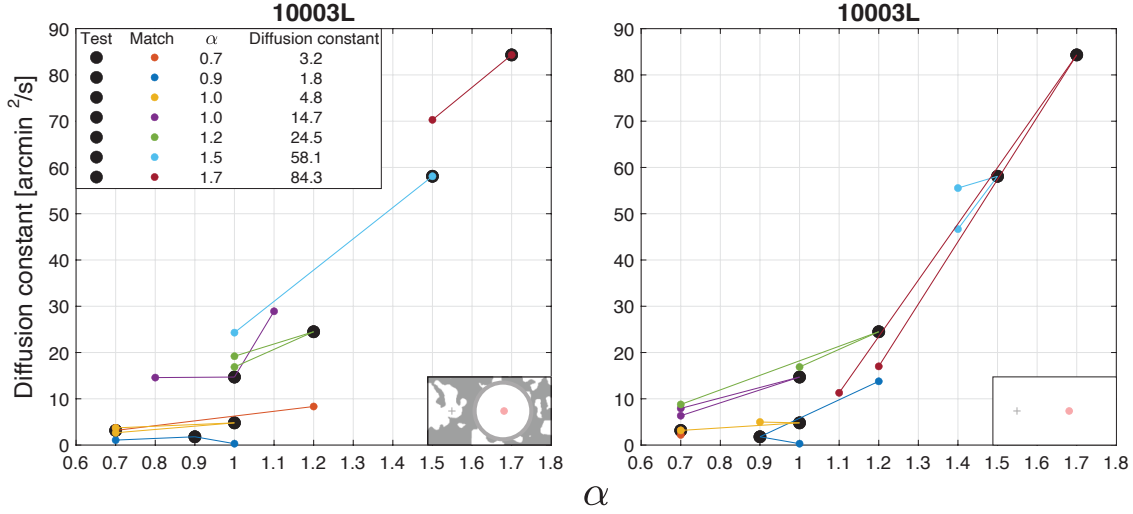


Figure 2.10: Matches from one subject tested under background-present and background-absent conditions. The conditions are indicated by labels on the bottom right corner of each graph. The large black circles are the tested α and diffusion constant values: 0.7 and 3.2 arcmin²/s, 0.9 and 1.8 arcmin²/s, 1.0 and 4.8 arcmin²/s, 1.0 and 14.7 arcmin²/s, 1.2 and 24.5 arcmin²/s, 1.5 and 58.1 arcmin²/s, and 1.7 and 84.3 arcmin²/s. The small circles are the two perceptual matches for each tested α and diffusion constant value.

black circles represent the tested α 's and diffusion constants and the small colored circles represent the subject's perceptual matches. For matches that deviated from the tested α and diffusion constant, the data points are connected to the respective black circle with a line of the same color. We found that sometimes the subject would correctly match the α and diffusion constant, while for other matches the values were both much higher or both much lower. For example, under background present conditions with tested α and diffusion constant equal to 1.7 and 84.3 arcmin²/s, respectively, the subject reached a perceptual match at these values as well as at 1.5 and ~ 70 arcmin²/s (Fig. 2.10, red). What could contribute to this mismatch, is that random walks with high α and diffusion constant values can be generated from the same average step length as random walks with low α and diffusion constant values, examples are shown in Fig. 2.1c. These results motivated us to constrain the random walk stimulus' α in the main experiments to be equal to one.

Methods: How we generated random walks with varying α 's and diffusion constants

Prior to the experiment, we pre-programmed 100s of 750-ms and 1500-ms duration random walks with varying α 's and varying diffusion constants for the subject to use in the matching task. The α 's ranged from 0.7 to 1.9 in increments of 0.1. These paths were generated by computing randomized step lengths in x and y drawn from a normal distribution with

a range of standard deviations from 0.05 to 1.6 arcminutes per step (or AOSLO frame), in increments of 0.05 arcminutes. For the sake of brevity, we will refer to the standard deviation of the randomized step lengths as simply *step lengths*. We converted the step lengths to polar coordinates to obtain the 2-dimensional step. Next, we selected the angle. All angles were equally probable for the first step. For all subsequent steps, when generating paths with α greater than one, each angle was drawn from a normal distribution with a mean equal to the angle of the previous step and with a standard deviation determined by the α . (When generating paths with α less than one, for all subsequent steps, each angle was drawn from a normal distribution with a mean equal to the angle of the previous step subtracted from 180° and with a standard deviation determined by the α .) The more the α deviated from one, the smaller the standard deviation. After generating all 2D steps and angles for the particular duration, we converted back to Cartesian coordinates by taking the cosine and sine of the angles and multiplying by the 2D steps to determine the x and y positions, respectively. The positions were successively added to generate the trajectory.

This process effectively randomized the length of each step. The direction was also randomized; however, as α deviated greater than one, the trajectory more likely moved in the same direction as the previous step; and, as α deviated less than one, the trajectory more likely moved in the opposite direction of the previous step. Owing to the random nature of generating paths in this method, the same randomized step length could generate a path with a range of possible diffusion constants and α 's. We computed the average diffusion constant for each step length and selected α , by inputting the step length as the ΔX and ΔY in the mean square displacement formula in Equation 1.2. After solving for the mean square displacement, we input this value as well as the selected α into Equation 1.1 to solve for the diffusion constant. For example, a step length of 1.6 arcminutes and α equal to 1.2 corresponded to a diffusion constant of $174.2 \text{ arcmin}^2/\text{s}$. Therefore, for each of the 32 step lengths, we generated 100 paths and from these, we selected the 10 paths with diffusion constants closest to the respective average diffusion constant and α 's closest to the selected α .

We used this method to also generate 50 trajectories for each selected α and diffusion constant tested. For each presentation, one of the 50 paths were selected randomly to present in the first interval.

Method of adjustment with a stimulus that moves orthogonal to eye motion with Gain +1.5

We performed a control experiment for one subject with the same method of adjustment protocol, except that we replaced the Gain 0 stimulus with a stimulus that moved orthogonal to eye motion with a Gain of +1.5. For brevity, we will refer to this stimulus as the *90° stimulus*. We expect that subjects will perceive motion as long as the stimulus moves in any direction other than in a direction consistent with retinal slip. If this is true, then the 90° stimulus would be perceived as moving similar to the Gain +1.5 stimulus.

World motion of the retina contingent stimuli

Undergoing the same retinal motion, the Gain -1.5 , Gain $+1.5$, and 90° stimuli move equally in the world. Said another way, the D_{WM} of the Gain -1.5 , Gain $+1.5$, and 90° stimuli are equal. However, note that these stimuli move in different directions: the Gain -1.5 and Gain $+1.5$ move opposite to each other, and the 90° stimulus moves orthogonal to both.

Retinal motion of the retina contingent stimuli

Undergoing the same retinal motion, the Gain -1.5 , Gain $+1.5$, and 90° stimuli move differently on the retina. A Gain -1.5 stimulus moves across the retina with 2.5x more motion than a natural, world-fixed stimulus. A Gain $+1.5$ stimulus has half the retinal motion of a world-fixed stimulus. A 90° stimulus moves with $(\sqrt{1.5^2 + 1^2})x$ more retinal motion than a world-fixed stimulus. For example, if the retina moved 1' right, the stimulus would move 1.5' up in the world. The retinal motion would be the Euclidean distance. The Gain -1.5 stimulus would have the highest retinal motion (D_{RM}), followed by a 90° stimulus, followed by a world-fixed stimulus, followed by a Gain $+1.5$ stimulus.

Results

Fig. 2.11 plots the diffusion constants of the retina contingent stimulus' perceived motion (D_{PM}) as a function of the world motion (D_{WM}). The red arrows show the extent to which the eye motion, and consequent retina-contingent stimulus' world motion (α_{WM}), deviated from Brownian. Arrows pointing right indicate persistence ($\alpha_{WM} > 1$), arrows pointing left indicate antipersistence ($\alpha_{WM} < 1$), and no arrow means that the motion was Brownian ($\alpha_{WM} = 1 \pm 0.02$). Under background-present conditions (Fig. 2.11, left), a paired t-test revealed no significant difference in the perceived motion between the Gain $+1.5$ stimulus and 90° stimulus ($p = 0.18$). Both perceived motions were significantly greater than that of the Gain -1.5 stimulus ($p = 0.0031$ Gain $+1.5$; $p = 0.00030$ 90° stimulus). Yet, the trends were different under background-absent conditions (Fig. 2.11, right). The Gain -1.5 stimulus now appeared to be moving the most, followed by the 90° stimulus, followed by the Gain $+1.5$ stimulus. The perceived motion of the Gain -1.5 stimulus was significantly greater than that of the 90° stimulus ($p = 0.02$, paired t-test). The perceived motion of the 90° stimulus was significantly greater than that of the Gain $+1.5$ stimulus ($p = 0.01$, paired t-test).

Method of adjustment with 750-ms duration intervals under background-present conditions

In the main study, the stimuli were presented for 1500-ms under background-present conditions and for 750-ms under background-absent conditions. We performed a control experiment for two subjects with the same method of adjustment protocol, except that we

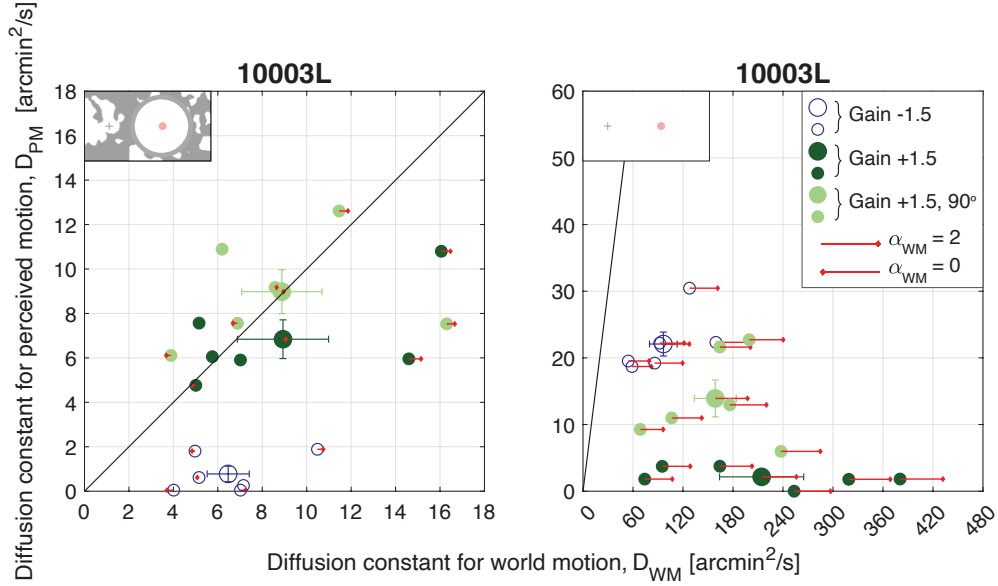


Figure 2.11: Individual results from one subject tested under background-present and background-absent conditions. The conditions are indicated by labels on the top left corner of each graph. The small circles are the six perceptual matches for Gain -1.5 stimuli (blue open symbols), Gain $+1.5$ stimuli (dark green filled symbols), and Gain $+1.5, 90^\circ$ stimuli (light green filled symbols). The large circles are the averages of the matches with standard error of the mean bars. The red arrows show the extent to which the eye motion, and consequent retina-contingent stimulus' world motion (α_{WM}), deviated from Brownian. Arrows pointing right indicate persistence ($\alpha_{WM} > 1$), arrows pointing left indicate antipersistence ($\alpha_{WM} < 1$), and no arrow means that the motion was Brownian ($\alpha_{WM} = 1 \pm 0.02$). Longer arrows correspond to higher deviations from Brownian motion. The arrow length in the legend indicates pure persistence ($\alpha_{WM} = 2$, straight line trajectory at constant velocity) if pointing right or pure antipersistence ($\alpha_{WM} = 0$, oscillatory motion) if pointing left.

presented the stimuli for a 750-ms duration under background-present conditions. This experiment verified that the different durations did not contribute significantly to the results. For each subject, a paired t-test comparing the diffusion constants for perceived motion (D_{PM}) revealed that, similar to the 1500-ms duration results, stimuli moving in advance of eye motion (Fig. 2.12, Gain $+1.5$) were seen as moving significantly more than stimuli moving in a direction consistent with retinal slip (Fig. 2.12, Gain -1.5) (10003L: $p = 0.0057$ and 20114R: $p = 0.042$).

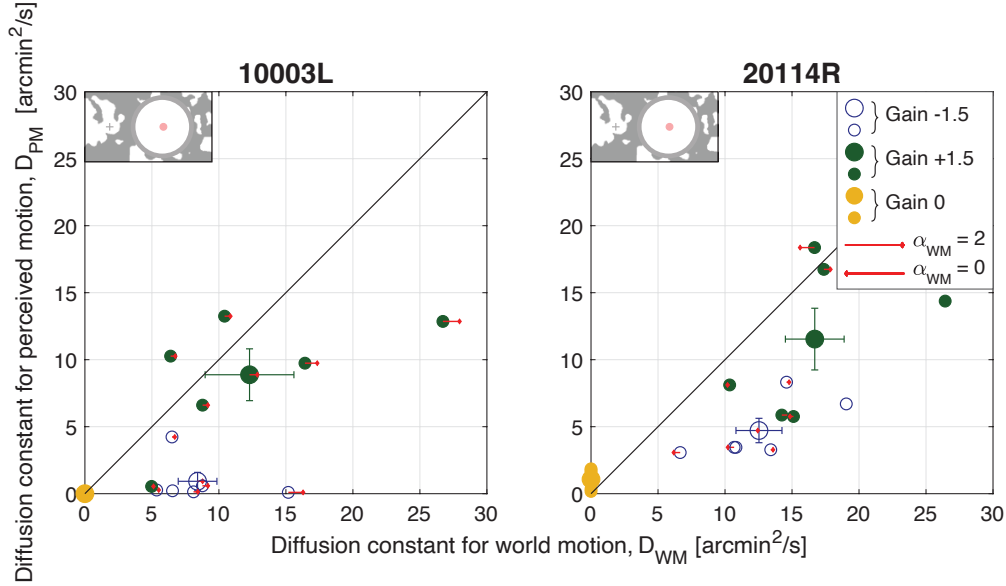


Figure 2.12: Individual results from two subjects tested under background-present conditions with 750-ms stimulus duration intervals. The condition is indicated by labels on the top left corner of each graph. The small circles are the six perceptual matches for Gain -1.5 stimuli (blue open symbols), Gain $+1.5$ stimuli (green filled symbols), and Gain 0 stimuli (yellow filled symbols). The large circles are the averages of the matches with standard error of the mean bars. The red arrows show the extent to which the eye motion, and consequent retina-contingent stimulus' world motion (α_{WM}), deviated from Brownian. Arrows pointing right indicate persistence ($\alpha_{WM} > 1$), arrows pointing left indicate antipersistence ($\alpha_{WM} < 1$), and no arrow means that the motion was Brownian ($\alpha_{WM} = 1 \pm 0.02$). Longer arrows correspond to higher deviations from Brownian motion. The arrow length in the legend indicates pure persistence ($\alpha_{WM} = 2$, straight line trajectory at constant velocity) if pointing right or pure antipersistence ($\alpha_{WM} = 0$, oscillatory motion) if pointing left.

Method of adjustment with the fixation cross remaining on during the random walk interval under background-absent conditions

In the original experiments tested under background-absent conditions, the fixation target was turned off during both the retina-contingent interval and the random walk interval. Because there was no frame of reference during the random walk interval, we could not truly assess the amount of motion perceived. Specifically, we could not conclude that the subject did not perceive motion when they matched a Gain 0 stimulus to a non-moving stimulus in the second interval. We performed a control experiment for one subject with the same method of adjustment protocol, except that the fixation target remained on to serve as a frame of reference during the second interval where they made the match (Fig. 2.13b).

We confirmed that the subject perceived almost no motion when they viewed a Gain 0

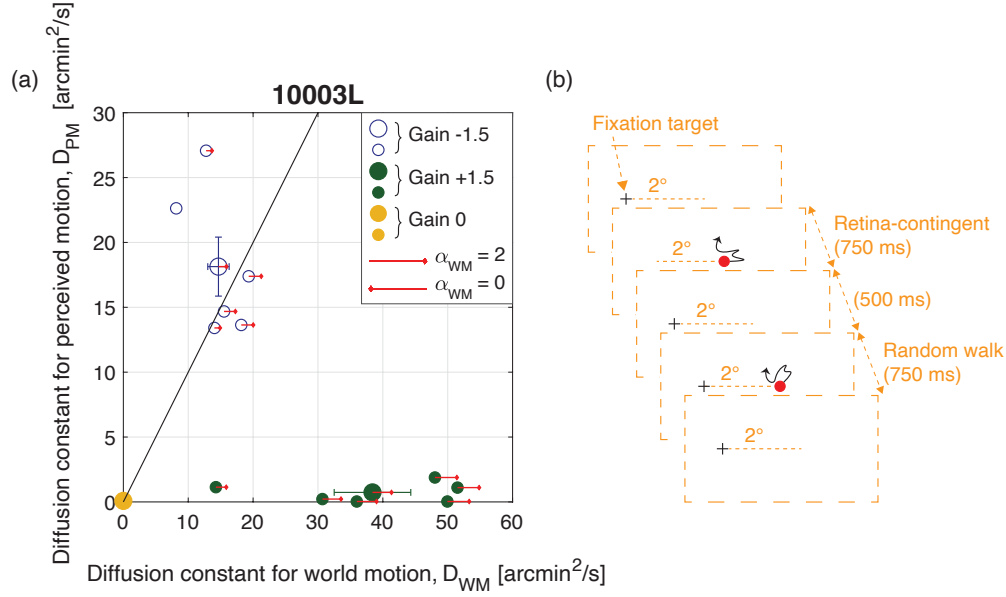


Figure 2.13: Control experiment tested under background-absent conditions. (a) Results from one subject. The small circles are the six perceptual matches for Gain -1.5 stimuli (blue open symbols), Gain $+1.5$ stimuli (green filled symbols), and Gain 0 stimuli (yellow filled symbols). The large circles are the averages of the matches with standard error of the mean bars. The red arrows show the extent to which the eye motion, and consequent retina-contingent stimulus' world motion (α_{WM}), deviated from Brownian. Arrows pointing right indicate persistence ($\alpha_{WM} > 1$), arrows pointing left indicate antipersistence ($\alpha_{WM} < 1$), and no arrow means that the motion was Brownian ($\alpha_{WM} = 1 \pm 0.02$). Longer arrows correspond to higher deviations from Brownian motion. The arrow length in the legend indicates pure persistence ($\alpha_{WM} = 2$, straight line trajectory at constant velocity) if pointing right or pure antipersistence ($\alpha_{WM} = 0$, oscillatory motion) if pointing left. (b) Experimental sequence. The fixation target remained on during the random walk interval.

stimulus under background-absent conditions (Fig. 2.13a). A paired t-test comparing the Gain 0 diffusion constants for perceived motion (D_{PM}) revealed no significant differences whether the fixation target was on (Fig. 2.13a) or off (Fig. 2.8, 10003L background-absent) during the random walk interval ($p = 0.78$).

2.9 Appendix 4: An Alternative Perceived Motion

The subject's task was to match the motion of a random walk stimulus to the perceived motion of a stimulus that was moving contingent to their drift motion. We computed a diffusion constant of the random walk stimulus to characterize the perceived motion (D_{PM}) of the retina contingent stimulus and we computed a diffusion constant of the retina-contingent

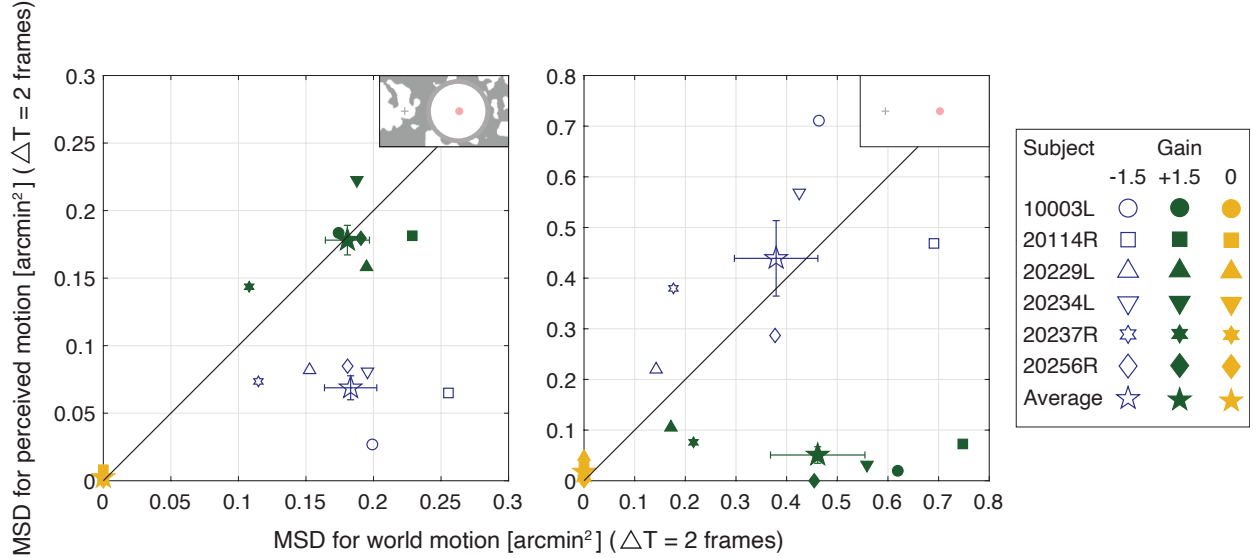


Figure 2.14: An alternative perceived motion analysis evaluating the mean square displacement (MSD) over a time interval (ΔT) of 2 frames. This parameter, denoted $MSD_{\Delta T=2frames}$, is defined with units of arcmin^2 . Average $MSD_{\Delta T=2frames}$ for perceived motion versus $MSD_{\Delta T=2frames}$ for world motion from six subjects. Experiments were tested under background-present and background-absent conditions, indicated by labels on the top right corner of each graph. The small symbols represent each subject’s average perceptual match for Gain -1.5 stimuli (blue open symbols), Gain $+1.5$ stimuli (green filled symbols), and Gain 0 stimuli (yellow filled symbols). The large stars are the group averages with standard error of the mean bars.

stimulus’ motion in the world (D_{WM}). Since the eye motion and consequent retina-contingent stimulus’ world motion sometimes deviated from Brownian, we computed a second parameter α . Fig. 2.4 shows that the α for eye motion (α_{EM}) was mostly persistent, reaching up to ~ 1.7 for subject 20237R under background-absent conditions. (Note that $\alpha = 2$ is a straight line trajectory at constant velocity). But we chose to constrain the motion of the random walk stimulus to be Brownian ($\alpha_{PM} = 1$) to ensure that the task was not overly complex. Thus, this method to quantify perceived motion is challenging, since the α_{PM} and α_{WM} were often times different.

To address this challenge, we performed a new analysis aiming to better quantify the perceived and world motion. In this analysis, we evaluated the mean square displacement (MSD) over a time interval (ΔT) of 2 frames (~ 33 milliseconds), using Equation 1.2 in Chapter 1. This parameter, denoted $MSD_{\Delta T=2frames}$, is defined with units of arcmin^2 .

We used a ΔT of 2 frames since our analysis with the model in Fig. 2.6 indicated that subjects tended to make motion judgments over a window of 2 frames (~ 33 milliseconds). A more detailed description of our motivation for selecting this ΔT is as follows: Fig. 2.6 plots

the ratios from Fig. 2.3 as a function of each subject's α_{WM} . The random walk stimulus' α , which represents the α for perceived motion (α_{PM}), is equal to one (Brownian motion) while the retina-contingent stimulus' α_{WM} ranges from antipersistent ($0.9 \leq \alpha_{WM} < 1$), to Brownian ($\alpha_{WM} = 1$), to persistent ($1 < \alpha_{WM} \leq 1.8$). This model shows how the ratio of the diffusion constants would vary with α_{WM} under a specific condition where the subject equated the mean square displacement (MSD) between the motion of the retina-contingent stimulus and the motion of the random walk stimulus with a specific ΔT . We tested a range of ΔT 's and determined by a least-squares procedure that a ΔT of 2 frames best predicted the measured data. This suggests that the subjects on average made motion judgments over a ΔT of 2 frames (~ 33 milliseconds).

We computed the $MSD_{\Delta T=2frames}$ across the random walk stimulus' motion traces at the setting of a perceptual match, to quantify the perceived motion of the retina-contingent stimulus. We computed the $MSD_{\Delta T=2frames}$ across the retina-contingent stimulus motion traces, to quantify the world motion of the retina-contingent stimulus. Fig. 2.14 plots the average $MSD_{\Delta T=2frames}$ for perceived motion vs the average $MSD_{\Delta T=2frames}$ for world motion, both expressed in arcmin^2 . Each small data point represents one subject and is the average of six trials. Refer to Fig. 2.15 for individual subject distributions of the six trials. The large stars represent the group averages with standard error of the mean bars. The data points that lie along the diagonal 1:1 line represent trials where the perceived motion of the retina-contingent stimulus was equivalent to the stimulus' actual motion occurring in the world. For Gain +1.5 under background-present conditions, we would expect that the motion that the subjects perceived would be equal to the motion of the stimuli in the world, and the results in Fig. 2.14 are consistent with this expectation.

When quantifying perceived motion using a diffusion constant, shown in Fig. 2.8, most of the subjects' perceived motion lied below the diagonal 1:1 line. Reasons may include differences between α_{PM} and α_{WM} , as well as the tendency to make motion judgments over shorter time intervals. Further discussion of these factors will be presented in **Chapter 3, Appendix 2: Comparison with the Results in Chapter 2**. This alternative analysis may be a better method to characterize perceived motion when α_{PM} and α_{WM} differ and when motion judgments are made over shorter intervals.

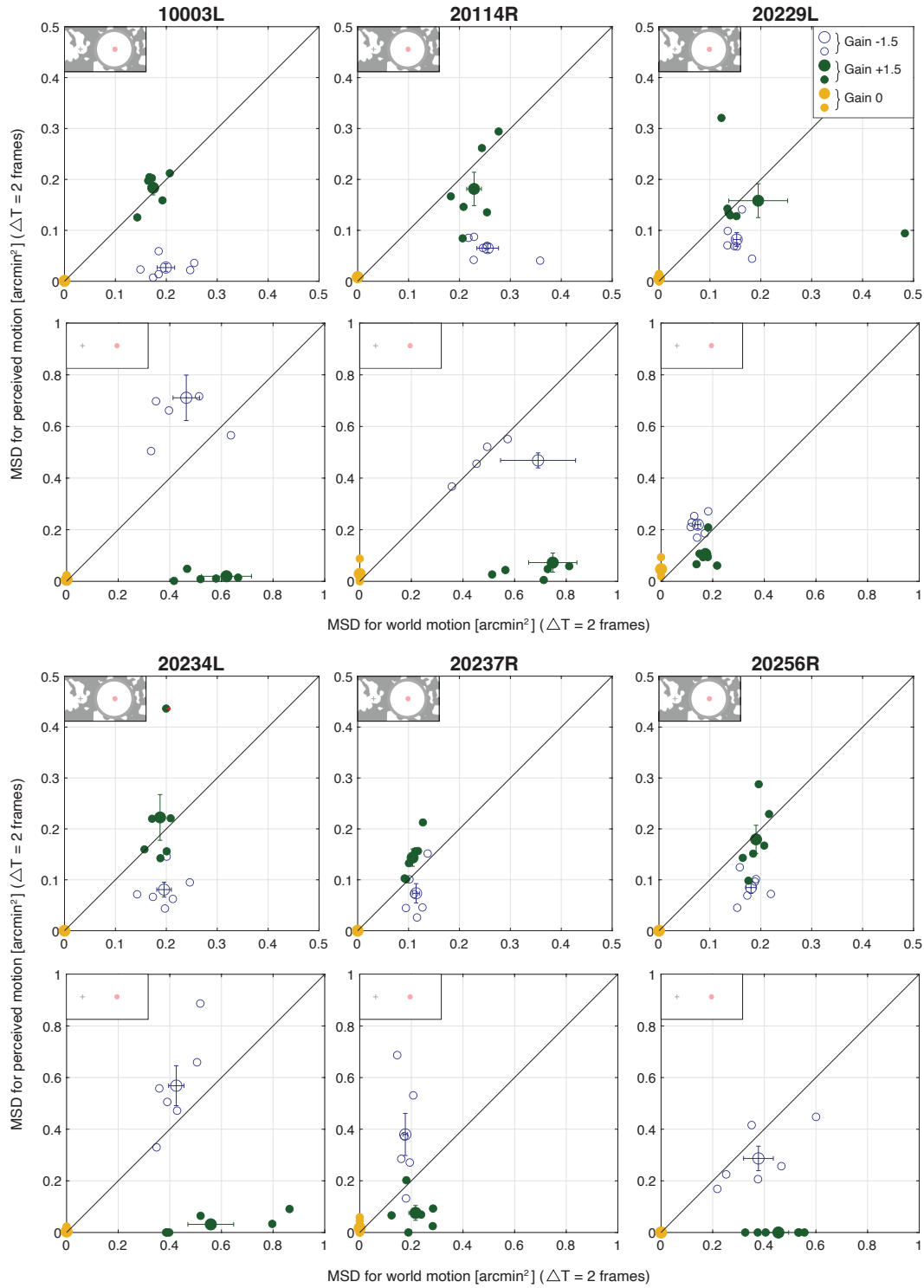


Figure 2.15: An alternative perceived motion analysis evaluating the mean square displacement (MSD) over a time interval (ΔT) of 2 frames. Individual results from six subjects tested under background-present and -absent conditions, indicated by labels on the top left corner of each graph. The small circles are the six perceptual matches for Gain -1.5 stimuli (blue open symbols), Gain $+1.5$ stimuli (green filled symbols), and Gain 0 stimuli (yellow filled symbols). The large circles are the averages with standard error of the mean bars.

Acknowledgments.

We are grateful to Prof. Jorge Otero-Millan, Prof. Hannah E. Smithson, and Dr. Allie C. Schneider for their helpful discussions. This research was supported by funding from NIH R01EY023591 and NIH T32 EY007043.

Competing Interests.

P.T. and A.R. are co-inventors on US Patent #10130253, assigned to the University of California.

Author Contributions.

This chapter is an edited version of the paper published in 2024. We added a new section, **Appendix 4: An Alternative Perceived Motion**. J.C.D., P.T., R.J.W., D.W.A., and A.R. designed research; J.C.D. and A.R. performed research; J.C.D. and A.R. analyzed data; P.T. and R.J.W. provided critical technical support; and J.C.D., D.W.A., and A.R. wrote the paper.

Citation for This Paper

D'Angelo, J. C., Tiruveedhula, P., Weber, R. J., Arathorn, D. W., & Roorda, A. (2024). A paradoxical misperception of relative motion. *Proc. Natl. Acad. Sci. U.S.A.*, 121(48), e2410755121.

Chapter 3

A discontinuity in motion perception during fixational drift

3.1 Abstract

The human visual system is tasked with perceiving stable and moving objects despite ever-present eye movements. Normally, our visual system performs this task exceptionally well; indeed, under conditions with frames of reference, our ability to detect relative motion exceeds the sampling limits of foveal cones. However, during fixational drift, if an image is programmed to move in a direction consistent with retinal slip, little to no motion is perceived, even if this motion is amplified. We asked: Would a stimulus moving in a direction consistent with retinal slip, but with a smaller magnitude across the retina, also appear relatively stable? We used an adaptive optics scanning light ophthalmoscope to deliver stimuli that moved contingent to retinal motion and measured subjects' perceived motion under conditions with world-fixed background content. We also tested under conditions with background content closer to and farther from the stimuli. We found a sharp discontinuity in motion perception. Stimuli moving in a direction consistent with retinal slip, no matter how small, appear to have relatively little to no motion; while, stimuli moving in the same direction as eye motion appear to be moving. Displacing background content to greater than 4° from the stimuli diminishes the effects of this phenomenon.

3.2 Introduction

Our eyes are never stable, even when fixating on a small target they make continuous miniature movements [44, 67, 75]. Despite this constant self-motion, the human visual system in general can properly perceive stable objects as stable and can detect moving objects with a level of precision that surpasses the sampling limits of the photoreceptors [88]. To achieve this, the visual system requires world-fixed visual content which serves as a frame of reference [42].

Yet, there exists a paradoxical exception: an image moving in a direction consistent with the direction of retinal slip appears relatively stable as long as the visual scene is filled with world-fixed retinal image background content [5, 17, 70]; and when all visual content is removed, this same image appears to be moving with a significantly higher magnitude of motion, a result discussed in Chapter 2 [17]. This phenomenon suggests that information from the retinal image informs the visual system about its direction of eye motion, and renders everything in the perceived image that is moving in a direction consistent with retinal slip as being relatively stable.

The retinal contribution to stable motion perception aligns with conclusions from a series of investigations by Murakami, Cavanagh and colleagues [55, 56, 59] with the caveat that the retina-derived signal also drives the “illusion of relative stability” that we report here and in previous papers. Retinal contributions to motion perception are also increasingly implicated in saccade detection and/or suppression. It has been found that the spatial frequency content of background image content on the retina affects saccadic suppression in human psychophysical measures as well as in retinal electrophysiology [36]. It has also been shown that images moving across the retina in a manner that is consistent with saccades but not driven by saccades elicit similar levels of saccadic suppression [73].

The illusion of relative stability suggests that there is a discontinuity in motion perception during drift, where direction is the critical parameter that governs how motion is perceived. Specifically, for images moving in a direction consistent with retinal slip, little to no motion is perceived, and for images moving in any other direction, the motion is readily detectable. In this present study, we assessed the sharpness of this discontinuity by measuring the perceived motion of stimuli that moved in a direction consistent with retinal slip with decreasing magnitudes, and of stimuli that moved in the same direction as eye motion. Next, we determined the extent to which the world-fixed retinal image background content drives this phenomenon by performing a second experiment in which we varied the proximity of the background content to the stimuli.

This work builds upon our understanding of this paradoxical phenomenon that disrupts our hyperacute sensitivity to detect relative motion. We make the following new contributions:

1. Our findings suggest a sharp discontinuity in motion perception during fixational drift. Even a stimulus moving in the same direction as eye motion but with a slower speed, and therefore slipping opposite to eye motion with 10% of the retinal motion of a world-fixed stimulus, appears relatively stable.
2. We discovered that, even if a stimulus is moving on top of or very close to high-contrast, high-spatial-frequency, world-fixed edges, as long as it moves opposite to eye motion, it appears relatively stable.
3. We determined that this phenomenon depends on the presence of retinal image background content within several degrees of the stimuli, and displacing background content beyond $\sim 4^\circ$ diminishes the effect.

Two objects moving in the same direction but with different retinal slip magnitudes is a unique and rare situation. We cannot think of a situation where this behavior we show here would have a functional use. Rather, we believe it is the exceptional outcome of a retina-based motion detection system that encodes directions and not magnitude for informing the percept.

3.3 Methods

Subjects.

Five subjects provided informed consent and participated in the experiments [subject number, age, sex]: [10003L, 58, M], [20237R, 27, F], [20255L, 24, M], [20256R, 23, F], and [20258R, 30, F]. One subject is a co-author on this paper and the other four subjects were experienced with psychophysical tasks. All procedures were approved by the Institutional Review Board at the University of California, Berkeley. Prior to the experiment, subjects applied one drop of 1% tropicamide and one drop of 2.5% phenylephrine hydrochloride to dilate and cycloplege.

Adaptive Optics Scanning Light Ophthalmoscopy.

Retinal imaging and stimulus delivery were performed using a multiwavelength AOSLO [54, 74]. Refer to Chapter 1, Section 1.1, for a full description of the system and its capability to perform real-time eye tracking.

Targeted Stimulus Delivery.

By recording the eye motion in real-time, the AOSLO can perform targeted stimulus delivery. As the 840-nm laser images the retina and the system recovers the eye motion in real-time, an AOM arms the 680-nm laser to deliver stimuli that move contingent to eye motion [6]. These stimuli are called “retina-contingent stimuli”. The use of narrow strips for registration combined with fast processing, enables a ~ 2 -ms lag between eye motion prediction and stimulus delivery [81, 82, 89].

A retina-contingent stimulus has a “Gain” which describes the stimulus’ world motion, that is contingent on the eye motion. The movements of the retina-contingent stimulus are equal to the eye movements multiplied by the Gain. The sign of the Gain indicates the direction the stimulus moves with respect to the eye movement. Gains < 0 move directly opposite to eye motion with amplified retinal slip. For example, the world motion of a Gain -1 stimulus is equal to -1 times the eye motion (Fig. 3.1B, *Panel 2*, purple arrow) and its motion across the retina is twice that of a world-fixed stimulus (Fig. 3.1B, *Panel 2*, dashed-brown arrow). Gain 0 describes a world-fixed stimulus, its world motion is equal to 0 times the eye motion (Fig. 3.1B, *Panel 3*, no purple arrow) and the stimulus naturally slips consistent to drift motion (Fig. 3.1B, *Panel 3*, dashed-brown arrow). Gain $+1$ describes a

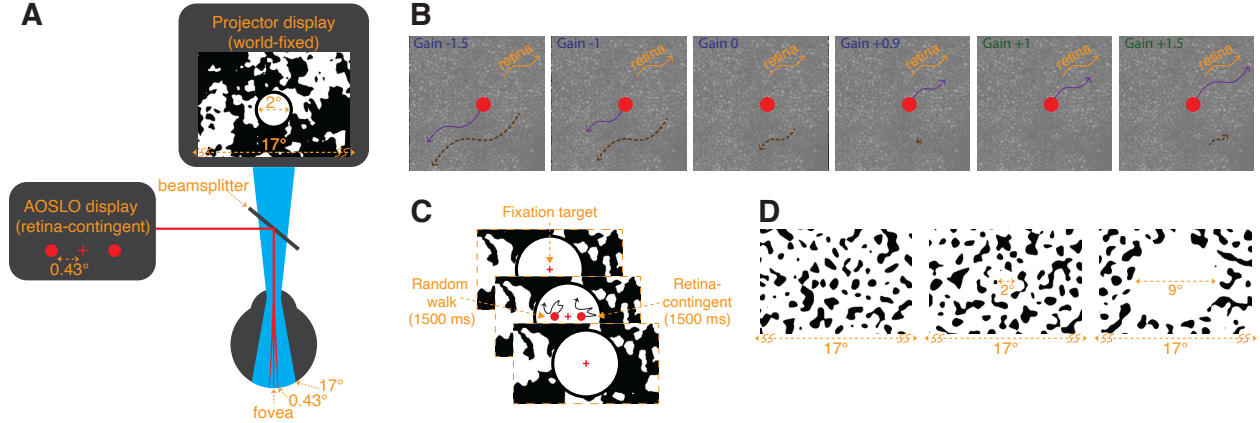


Figure 3.1: Display configuration. (A) The AOSLO drew three 680-nm stimuli: a central fixation cross, and two horizontally offset circular stimuli positioned 0.43° nasal and 0.43° temporal from the cross. Concurrently, over its 17° field of view, the projector displayed world-fixed patterns, dependent on the experiment. In Experiment 1, the background was filled with a blurred and binarized $1/f$ noise pattern with a 2° -diameter central white circle with a surrounding black ring that overlayed the 680-nm stimuli, shown in (A). In Experiment 2, the background was filled with a noise pattern that was generated by filtering white noise with a Gaussian bandpass filter at 0.5 cycles per degree (cpd) (0.5 cpd standard deviation), and binarizing the pattern, shown in (D). (B) Rules for the retina-contingent stimuli. Each panel shows examples of different retina-contingent stimuli undergoing identical retinal trajectories, indicated by the orange arrows. The purple arrows indicate the world trajectories of the retina-contingent stimuli. The dashed-brown arrows indicate the stimuli's image motion across the retina. Gains > 1 move in the same direction as eye motion (orange and dashed-brown arrows point in the same direction) while Gains < 1 move opposite to eye motion (orange and dashed-brown arrows point in opposite directions). (C) Experimental sequence. Subjects fixated on a world-stationary cross and initiated a 1500-ms presentation of two stimuli that moved with different rules. The left stimulus moved in a random walk, independent of eye motion, and the right stimulus moved contingent to eye motion with a Gain that ranged from -1.5 to $+1.5$. (D) Experiment 2 background conditions. The patterns extended over the full 17° field of view (*Left*), or surrounded a 2° -diameter white circular opening (*Middle*), or surrounded a 9° -diameter white circular opening (*Right*). The AOSLO stimuli were presented at the center of the displays and the subject performed the same experimental protocol shown in (C). For the no-white-circle and 2° -diameter white circle conditions, the fixation cross remained on for the entire duration. For the 9° -diameter white circle condition, the fixation cross turned off during the 1500-ms presentation of the stimuli.

stabilized stimulus, its world motion is equal to 1 times the eye motion (Fig. 3.1B, *Panel 5*, purple arrow) and therefore is locked in place on a region of the retina (Fig. 3.1B, *Panel 5*, no dashed-brown arrow). Gains $> +1$ move faster than the eye motion and in the same direction. For example, the world motion of a Gain $+1.5$ is equal to $+1.5$ times the eye motion (Fig. 3.1B, *Panel 6*, purple arrow) and its motion across the retina is half that of a world-fixed stimulus (Fig. 3.1B, *Panel 6*, dashed-brown arrow).

Note that Gains greater than 0 but less than $+1$ move in a direction consistent with the direction of retinal slip, but with reduced retinal slip compared to a world-fixed stimulus. For example, if the eye moves to the right by 10 arcmin, a Gain $+0.9$ stimulus would move right by 9 arcmin with retinal slip equal to 1 arcmin. Although both move in a direction consistent with retinal slip, Gain $+0.9$ has only 10% the retinal slip of a world-fixed stimulus. The retinal slip of the Gains 0 and $+0.9$ are illustrated by dashed-brown arrows in Fig. 3.1B in *Panels 3* and *4*, respectively. Gain $+1$ has zero retinal slip, and is therefore the transition point: For all Gains $< +1$ the stimulus' motion across the retina is in a direction directly opposite to eye motion, in a direction consistent with retinal slip; and for all Gains $> +1$, the stimulus' motion across the retina is in the same direction as eye motion.

Projector Display.

A digital light projector (Lightcrafter DLP4500; Texas Instruments, Dallas, TX, USA) was used to display a 17° background that was coaligned with the AOSLO beams (Fig. 3.1A). The average luminance was approximately 540 cd/m^2 . Background patterns were programmed with MATLAB (MathWorks, Natick, MA, USA) using the Psychophysics Toolbox [11, 39, 62].

Random Walk Analysis.

Fixational drift is similar to a random walk and the magnitude of drift can be quantified by computing a diffusion constant [14, 17]. Recent studies have found that drift motion is not truly random, instead having correlated or anti-correlated properties depending on the timescale [22, 24], which can be quantified by computing the parameter α [17, 22, 24, 71, 51]. Chapter 1, Section 1.1 describes the methods and equations for the statistical analyses we performed to evaluate the random walk motion. Across all traces from each analysis, we quantified the amount of motion (diffusion constant) and its deviation from Brownian motion (α). We performed this random walk analysis on the random walk stimulus' motion (D_{PM} and α_{PM} , where PM denotes perceived motion), the retina-contingent stimulus' motion (D_{WM} and α_{WM} , where WM denotes world motion), and the eye's motion (D_{EM} and α_{EM} , where EM denotes eye motion).

Generating Random Walks and Random Jitter.

Before the experiments, we generated 100s of 1500-ms duration random steps that were either cumulatively summed to produce random walks or concatenated to produce random jitter. The method to generate random walks is described more fully in Chapter 2 [17]. Briefly, step lengths in x and y were drawn from a normal distribution with standard deviations ranging from 0.05 to 1.6 arcmin per step in increments of 0.05 arcmin. We computed the average diffusion constant from the trajectories generated for each step length. This was achieved by first solving for the mean square displacement in Equation 1.2, where ΔX and ΔY are equal to the step length, and then using this result in Equation 1.1 to solve for the diffusion constant. For each step length, we generated 100 random walks and then selected 10 paths of the 100 which had diffusion constants closest to the respective average diffusion constant. The α of the random walks was approximately equal to one. To program random jitter, step lengths in x and y were drawn from a normal distribution with the following standard deviations: 0.1, 0.2, 0.3, and 0.4 arcmin per step. These steps were non-cumulative, meaning that each step began from the same starting position. Therefore, the α of the random jitter was approximately equal to zero.

Experimental Design.

Set Up.

Subjects' aligned the pupil of one eye with the AOSLO beam and covered their fellow eye with an eye patch. Dental bite bars were used to immobilize the head. The bite bar apparatus was adjusted in the X, Y, and Z dimensions to position the eye's entrance pupil at the exit pupil of the AOSLO and the projector to optimize wavefront correction performance and to optimize the image of the retina.

Experimental Procedure.

The subject was presented three 680-nm stimuli through the AOSLO: a central fixation cross, and two horizontally offset circular stimuli positioned 0.43° nasal and 0.43° temporal from the cross. The fixation cross subtended 5 arcmin and the circular stimuli subtended 6 arcmin. Concurrently, the projector displayed a 17° background that was superimposed with the AOSLO rasters (Fig. 3.1A).

In the first experiment, the background displayed a blurred and binarized 1/f noise pattern that changed after each presentation. A 2° -diameter white circle, with a 0.33° -wide black ring around it, was overlayed onto the AOSLO rasters, therefore canceling perception of the 840- and 940-nm rasters (Fig. 3.1A). The fixation cross remained on for the entire experiment.

In the second experiment, the background displayed a noise pattern that was generated by filtering white noise with a Gaussian bandpass filter at 0.5 cycles per degree (cpd) (0.5 cpd standard deviation), and then binarizing the pattern. We tested three background conditions:

extending over the full 17° field of view (Fig.3.1D, *Left*), or with a 2° -diameter white circular opening (Fig.3.1D, *Middle*), or with a 9° -diameter white circular opening (Fig.3.1D, *Right*). Similar to Experiment 1, the patterns changed after each presentation. Under the no-white-circle condition, the pattern extended over the AOSLO rasters, and therefore, the 840- and 940-nm rasters were dimly visible in the regions where the pattern was black (Fig.3.1D, *Left*). For the no-white-circle and 2° -diameter white circle conditions, the fixation cross remained on for the entire experiment while for the 9° -diameter white circle condition, the fixation cross turned off during the 1500-ms presentation of the stimuli. For the 2° - and 9° -diameter white circle conditions, the subjects' field of view was limited to only 17° . Using methods described in Chapter 2 [17], we set up a white paper with an aperture in front of the display permitting only the AOSLO and projector beams to enter the eye. Notably, the aperture in our experiment was wider than the one used in Chapter 2 [17] yielding, a full 17° view of the projector and AOSLO displays. LEDs were positioned between the subject and the paper to illuminate the paper. Due to its close proximity to the eye, the natural blur of the aperture in the paper rendered the transition between the display and luminance-matched paper invisible. The different choices for the binarized patterns from Experiment 1 and 2 yielded no difference in the results.

Retina-Contingent Conditions.

In the first experiment, we measured the perceived motion of multiple retina-contingent stimuli. The Gains of the stimuli ranged from -1.5 to $+1.5$ in increments of 0.25 . We additionally tested Gains $+0.85$, $+0.9$ and $+1.1$ to measure closer to Gain $+1$, the transition point between stimuli that move opposite to eye motion and stimuli that move in the same direction as eye motion. A total of sixteen Gains were tested and the subjects performed at least three trials per Gain. Subjects performed at least six trials of Gain $+1.25$ and $+0.75$. Subjects performed nine trials of Gain $+1$, to mitigate the effects of uncertainty due to fading (except for 10003L, who only performed six trials of Gain $+1$). In the second experiment, we tested only Gains -1.5 , 0 , and $+1.5$. Subjects performed two trials of Gain 0 and performed at least four trials of Gain -1.5 and $+1.5$ (except for 20237R, who only performed three trials for Gain -1.5 of the 9° -diameter white circle condition).

Task.

One Gain was tested per trial. In a single trial, the subject began by fixating on the 680-nm cross. Using a gamepad, the subject initiated a 1500-ms presentation of two horizontally offset circular 680-nm stimuli. The three 680-nm stimuli were programmed with different rules: the fixation cross remained stationary, the left stimulus moved in a pre-programmed random walk that was independent of eye motion, and the right stimulus moved contingent to the retina with a specific Gain (Fig. 3.1C). After attending to the circular stimuli, the subject adjusted the magnitude of motion of the left stimulus (random walk) until it matched that of the right stimulus (retina-contingent). The subject could initiate as many

presentations as they wished while making their adjustments. When they reached a match, they were instructed to initiate at least three more presentations before submitting their response. The subjects were not given any specific criteria to make the match and in general expressed satisfaction in their ability to achieve one. After submitting the trial, the subject proceeded to the next trial which tested a new retina-contingent stimulus with a specific Gain. The Gains were presented in a pseudorandom order across multiple sessions. This experimental protocol applied to both Experiments 1 and 2.

Eye and Stimulus Motion Traces.

From each presentation of the experimental sequence, we recorded a two-second duration video of the retina. Additionally, the system drew three digital markers that indicated the exact positions of the three 680-nm stimuli on each frame of the video. After the experiment, we extracted absolute eye motion traces from the videos through an offline software called ReVAS, which uses a similar cross-correlation method described in Chapter 1, Section **Real-time Eye Tracking** [2]. Next, we used an offline algorithm to locate and record the positions of the digital markers in each frame. The eye motion and stimulus motion traces were used for the following:

Quality Control.

First, we identified and removed videos where tracking failed. Tracking failure results in frames with no image captured or with poor image quality and ReVAS either fails to extract eye motion traces or produces fragmented traces. Tracking can fail for a variety of reasons: for example, if the subject blinks, saccades, or looks away from the fixation cross during the presentation. Dry tear film or a fallen eyelash can also disrupt the wavefront sensor and lead to tracking failures. These were usually recognizable to the subjects, who were instructed prior to the experiment to ignore presentations with poor tracking.

Second, we identified and removed videos where the tracking did not fail, but a microsaccade occurred during frames in which the stimuli were delivered. We kept a record of the number of videos per trial where a microsaccade occurred. Our goal was to measure the perceived motion during periods of fixational drift, and therefore including presentations with microsaccades would have confounded the analyses.

Third, we determined the number of videos where the tracking was poor but might not have been recognizable to the subject. This was achieved by comparing the retina-contingent stimulus motion trajectory to the eye motion trace. For every video, we computed the ideal retina-contingent stimulus motion trajectory computed from the eye motion trace and the specific Gain. For each frame, we computed the distances in x and y between the ideal retina-contingent position and the measured retina-contingent position. This distance represents the stimulus misdelivery, where greater distances indicate greater error in stimulus delivery. For each dimension, we took the standard deviation of the distances across all frames. If the standard deviation of the stimulus misdelivery in either the x or y dimension was greater

than 0.9 arcmin, we removed the video from further analysis. We tallied the number of poor videos – videos that had standard deviations greater than 0.9 arcmin or that contained microsaccades – and if this number was greater than half the total number of videos in the trial, we dropped the trial and the subject was invited back to repeat the trial.

Quantifying the Stimulus Delivery Error.

With the remaining traces, we quantified the magnitude of stimulus delivery error for each trial. Using the same method described in Section **Quality Control**, we computed the distances in x and y between the ideal retina-contingent position and the measured retina-contingent position. In a single trial, we computed the standard deviation of all distances in x and y across all frames from all videos. An example from one subject is shown in Fig. 3.2A, the red points indicate the standard deviation of error from a single trial and the black points indicate the average standard deviation of error across all trials. Note that this subject, 10003L, had the highest error out of the five subjects tested, with a maximum average standard deviation of error equal to ~ 0.48 arcmin, which is about the diameter of a foveal cone photoreceptor [86]. The results of all subjects can be found in Fig. 3.6 in Appendix 1.

Overall, the AOSLO real-time tracking system demonstrates subarcminute tracking accuracy. It is noted here that tracking can never be perfect because of the ~ 2 -ms latency between the last measurement of eye position and the delivery of the stimulus [6]. Any motion that occurs during the ~ 2 -ms lag will not be accounted for and thus manifests as error. Therefore, even in ideal conditions – high quality retinal images and slow drift motion – the latency can contribute some magnitude of stimulus delivery error.

Quantifying the Perceived Motion of the Retina-Contingent Stimuli.

After the experiment, we recovered the random walk stimulus traces at the setting of a perceptual match and computed a diffusion constant across these traces. The diffusion constant of the random walk stimulus represents the magnitude of motion that the subject perceived when they viewed the retina-contingent stimulus. We will refer to this value as the diffusion constant for perceived motion, or D_{PM} . An example from one subject is shown in Fig. 3.2C (yellow points) and for all subjects in Fig. 3.7 in Appendix 1.

Accounting for Motion Perception Due to Error.

Next, we were motivated to determine to what degree stimulus delivery errors, which were computed in Section **Quantifying the Stimulus Delivery Error**, contributed to the subjects’ motion judgments during the experiments. These errors manifest as approximately random, non-cumulative steps, or “jitter”, which are superimposed onto the retina-contingent stimulus’ motion. If the visual system indeed fully suppresses the perception of motion that

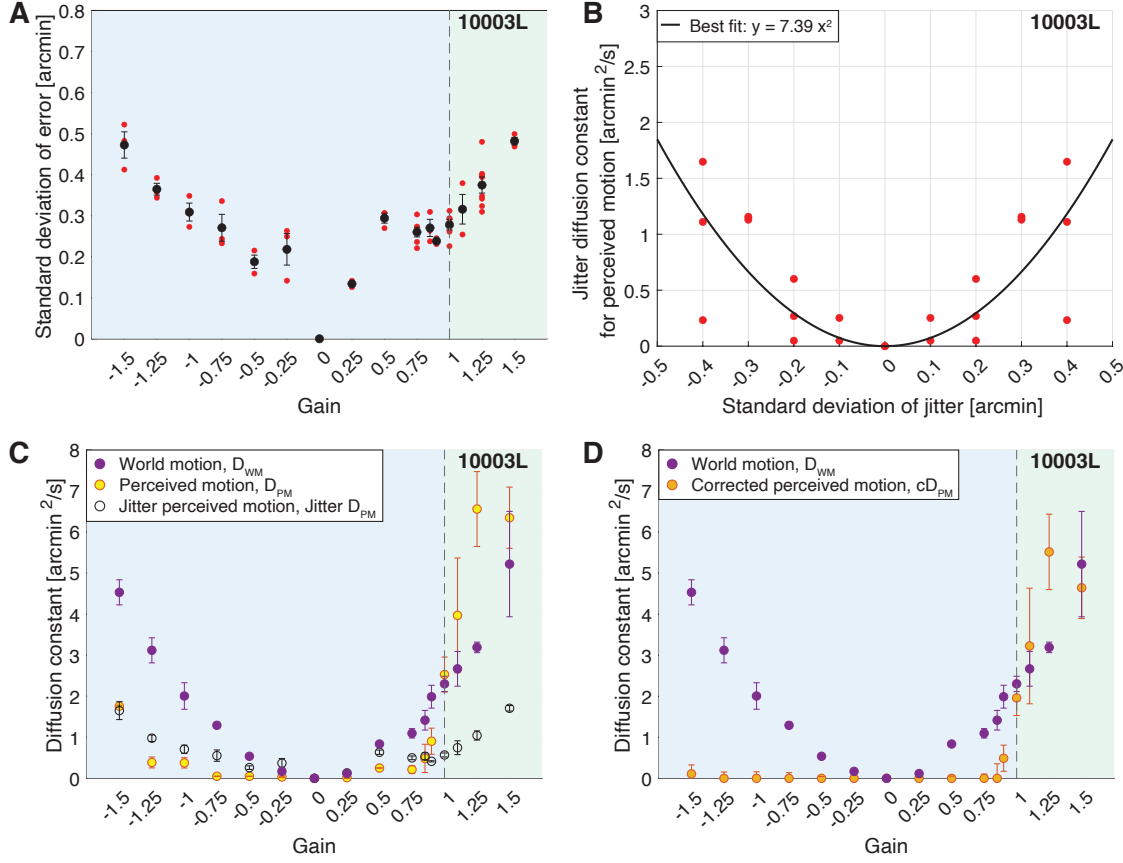


Figure 3.2: Results from subject 10003L. The blue region of graphs (A), (C) and (D) indicates the Gains where the stimulus' motion across the retina is in a direction that is directly opposite to eye motion. The green region indicates the Gains where the stimulus' motion across the retina is in the same direction as eye motion. (A) The magnitude of stimulus delivery error for each Gain. For each trial, we computed the distances in x and y between the ideal retina-contingent stimulus motion trace and the measured retina-contingent stimulus motion trace. The red points indicate the standard deviation of error from one trial – this is the standard deviation across the distances in x and y from all frames from all videos within a single trial. The black points indicate the average standard deviation of error across all trials, with SE of the mean bars. (B) Jitter diffusion constants for perceived motion, $Jitter D_{PM}$, plotted as a function of the standard deviation which was used to generate the jitter stimulus. Each red point represents one trial and was reflected across the y-axis. The black curve is a best-fit quadratic function which is anchored at 0 arcmin²/s. (C and D) Diffusion constants plotted as a function of the sixteen Gains. Purple points indicate average diffusion constants for world motion, D_{WM} , with SE of the mean bars. (C) Yellow points indicate average diffusion constants for perceived motion, D_{PM} , with SE of the mean bars. Black-hollow points indicate average $Jitter D_{PM}$ with SE of the mean bars, given the standard deviation of error in (A). (D) Orange points indicate average corrected diffusion constants for perceived motion, cD_{PM} , with SE of the mean bars. $cD_{PM} = D_{PM} - Jitter D_{PM}$.

is in a direction consistent with the direction of retinal slip, then it is possible that under these conditions, the motion that the subjects matched was solely influenced by the jitter due to the tracking errors.

To measure the perceived motion of jitter, we executed the same method-of-adjustment procedure, except that we replaced the retina-contingent stimulus with a stimulus that moved independently of eye motion. This stimulus jittered in place with step sizes in x and y that were determined by a standard deviation. We tested the following standard deviations: 0, 0.1, 0.2, 0.3, and 0.4 arcmin, refer to Section **Generating Random Walks and Random Jitter** for more details on the generation of this stimulus. Note that because subject 20237R’s average standard deviations of error were below 0.4 arcmin, we did not test this subject with a 0.4 arcmin standard deviation of jitter, shown in Fig. 3.6 in Appendix 1. Subjects were instructed to adjust the magnitude of motion of the random walk stimulus until it matched the perceived motion of the jitter stimulus. We computed a diffusion constant of the random walk stimulus at the setting of a perceptual match which represents the subjects’ perceived motion of the jitter stimulus. This value will be referred to as the Jitter diffusion constant for perceived motion, or *Jitter* D_{PM} . The subjects performed three trials for each standard deviation condition. Fig. 3.2B plots the *Jitter* D_{PM} as a function of the standard deviations for one subject. We reflected the results across the y-axis and fit a quadratic function across the data points. Because perceived motion cannot be negative, we anchored the function to 0 arcmin²/s using the MATLAB function `polyfitZero` [52]. Results for all subjects are reported in Fig. 3.6 in Appendix 1.

Using methods described in Section **Quantifying the Stimulus Delivery Error**, for each subject, we determined the magnitude of stimulus delivery error for each Gain (Fig. 3.2A). Using the subjects’ perceptual responses of the jitter stimulus (black curve in Fig. 3.2B), we estimated the perceived motion of this stimulus delivery error (black points in Fig. 3.2A). For example, for 10003L, the average standard deviation of stimulus delivery error during presentations of Gain -1.5 stimuli was ~ 0.47 arcmin (Fig. 3.2A) which corresponded to an approximate perceived motion of 1.65 arcmin²/s (Fig. 3.2B).

The following were computed for each subject. For each Gain, we averaged the diffusion constants for perceived motion of the retina-contingent stimulus (average D_{PM} , Fig. 3.2C, yellow points) and we averaged the perceived motion of error (*Jitter* D_{PM} , Fig. 3.2C, black-hollow points). We subtracted average $D_{PM} - \text{average } \textit{Jitter } D_{PM}$, and the result will be referred to as the “corrected diffusion constant for perceived motion”, or cD_{PM} . Negative cD_{PM} values were set equal to 0 because motion perception cannot be negative. Fig. 3.2D shows the average cD_{PM} for one subject and Fig. 3.3A and Fig. 3.7 in Appendix 1 show the average cD_{PM} for all subjects.

Quantifying the World Motion of the Retina-Contingent Stimuli.

We collected the retina-contingent stimulus motion traces from every video within a trial, excluding videos that were removed after the filtering steps in Section **Quality Control**. We computed the diffusion constant across all traces within each trial and this value will

be referred to as the diffusion constant for world motion of the retina-contingent stimulus, or D_{WM} . Fig. 3.2 *C* and *D* show the average D_{WM} for one subject and Fig. 3.3*A* and Fig. 3.7 in Appendix 1 show the average D_{WM} for all subjects. Observe that while the instantaneous speed of the stimulus motion increases linearly with the magnitude of the Gain, the associated diffusion constants increase with the square of the Gain.

Ratio Analysis.

For each subject we performed the following: For each Gain, we computed the ratio of the [average corrected diffusion constant for perceived motion] to the [average diffusion constant for world motion], or average cD_{PM}/D_{WM} . Because world-fixed stimuli have $D_{WM} = 0$ arcmin²/s, we removed the ratios for Gain 0. Fig. 3.3*B* shows the average cD_{PM}/D_{WM} for each subject, and Fig. 3.8 in Appendix 1 reports the individual trial distributions of cD_{PM}/D_{WM} for all subjects. We expect the ratio to be one if subjects perceived the motion veridically. Ratios less than one indicate that subjects underestimated the motion and ratios greater than one indicate that subjects overestimated the motion.

Model Comparison Metric.

We performed multiple function fits to the ratios in Fig. 3.3*B* to assess the sharpness of the discontinuity in motion perception during drift, where x represents the Gain and y_i represents the average cD_{PM}/D_{WM} . If the discontinuity is sharp, then the data would be best fit with two independent functions on either side of a breakpoint. To evaluate the different fits, we computed the least squares (corrected) Akaike information criterion or AIC_c . This model comparison metric evaluates goodness-of-fit while penalizing models with increasing number of parameters. As recommended by Burnham & Anderson [12], the AIC is added to a penalty term to reduce small-sample bias. After computing the AIC_c for each model, we computed evidence ratios to assess the strength of evidence for each model, using methods described in Burnham & Anderson [12]. Higher evidence ratios indicate stronger evidence for the “best” model. Lower evidence ratios indicate weaker support for the “best” model and suggests more uncertainty for model selection [12]. An extended description of the models and the equations for the AIC_c and evidence ratio are reported in Appendix 1.

Statistics.

For Experiment 2, we performed a 2-factor, repeated-measures ANOVA of the diffusion constant for eye motion (D_{EM}), α for eye motion (α_{EM}), and corrected diffusion constant for perceived motion (cD_{PM}). There were 3 Gains (-1.5 , 0 , and $+1.5$) and three background conditions (no-white-circle, 2° -diameter white circle, and 9° -diameter white circle conditions), which were within-subject factors. If the repeated-measures ANOVA found an effect, indicated by $P < 0.05$, we performed a post hoc Tukey-Kramer test to measure the significance of the pairwise comparisons.

3.4 Results

Experiment 1.

Fig. 3.3A plots the average diffusion constants as a function of the sixteen Gains for the five subjects. The orange points indicate average corrected diffusion constants for perceived motion, cD_{PM} , of the retina-contingent stimuli. The purple points indicate average diffusion constants for world motion, D_{WM} , of the retina-contingent stimuli. Each point represents one subject and is the average across at least three trials.

Fig. 3.3B plots the average cD_{PM}/D_{WM} as a function of the sixteen Gains for the five subjects. A cD_{PM}/D_{WM} equal to one indicates that the subject perceived the stimulus' actual motion in the world, a cD_{PM}/D_{WM} lower than one indicates that the subject underestimated the world motion, and a cD_{PM}/D_{WM} greater than one indicates that the subject overestimated the world motion.

A Sharp Discontinuity in Motion Perception During Drift.

We performed multiple fits to the ratios in Fig. 3.3B to assess the sharpness of the discontinuity in motion perception during drift. We tested linear fits on either side of a breakpoint, the breakpoints ranged from Gain -0.75 to $+1.1$. We tested single-parameter linear fits as well as two-parameter linear fits in slope-intercept form. We tested a quadratic curve to the left of the breakpoint and a single-parameter linear fit to the right. Last, we tested a single fit across all ratios: a quadratic, a cubic, and a quartic function. Examples are shown in Fig. 3.3B and Fig. 3.9 of Appendix 1.

The corrected Akaike information criterion (AIC_c) values are lowest ("best") for two models: a quadratic curve to the left of Gain $+1$ and a single-parameter linear fit to the right, as well as single-parameter linear fits on either side of Gain $+1$; both models are shown in Fig. 3.3B. The evidence ratios for these models are 1 and 1.57, respectively. The third lowest AIC_c value is from a model with two-parameter linear fits on either side of a breakpoint at Gain $+1$, although its evidence ratio is ~ 6.11 suggesting that there is little evidence in favor of this model. The AIC_c values for all other models are more positive with evidence ratios greater than 200, meaning that evidence is reasonably strong against these models. Thus, given the dataset and the models tested, these model evaluation metrics suggest that there is reasonably strong evidence that either of the top two performing models are the "best" fit, although there is high uncertainty which of these two is the "best". Our results suggest that there is a sharp discontinuity in motion perception during drift where direction with respect to eye motion is the critical parameter in governing how motion is perceived. Stimuli moving opposite to eye motion (Gains < 1) are underestimated, while stimuli moving in the same direction as eye motion (Gains ≥ 1) are perceived as moving, and the motion perceived is similar to the stimulus' actual motion in the world ($\sim 0.86x$). Model comparison metrics for all models are reported in Table 3.1 in Appendix 1. We additionally performed the same calculations using the original, uncorrected diffusion constants for perceived motion (D_{PM})

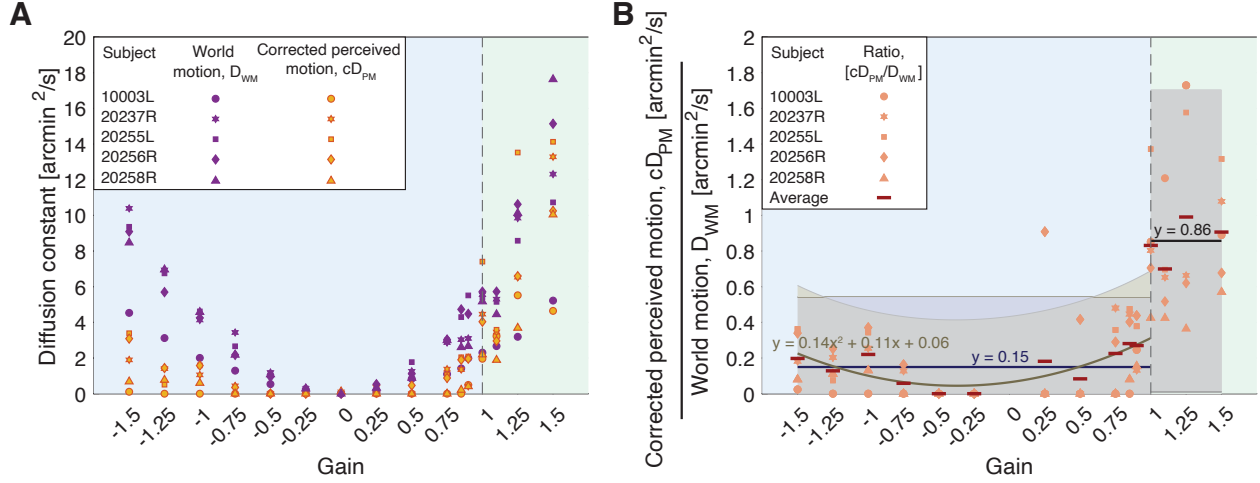


Figure 3.3: Experiment 1: Perceived motion and world motion of the retina-contingent stimuli. The blue regions indicate the Gains where the stimulus' motion across the retina is in a direction that is directly opposite to eye motion. The green regions indicate the Gains where the stimulus' motion across the retina is in the same direction as eye motion. (A) Diffusion constants from five subjects as a function of the Gains. Orange points indicate average corrected diffusion constants for perceived motion, cD_{PM} . Purple points indicate average diffusion constants for world motion, D_{WM} . Each point represents one subject and is the average across all matches. (B) Average cD_{PM}/D_{WM} from five subjects as a function of the Gains. Each point represents one subject and is the average ratio across all matches. The red bars indicate the average ratio across all subjects. Note that ratios for Gain 0 were removed. To the ratios of Gains < +1, we fit a quadratic curve ($y = 0.14x^2 + 0.11x + 0.06$) as well as a single-parameter line ($y = 0.15$). To the ratios of Gains ≥ +1, we fit a single-parameter line ($y = 0.86$). The intervals indicate the 95% confidence bounds of the fits.

in place of the cD_{PM} of the ratio, and we found the same trends, which are reported in Table 3.2 in Appendix 1.

Experiment 2.

Fig. 3.4 plots the average diffusion constants for each of the three Gains tested (Gains -1.5, 0 and +1.5) under three background conditions (no-white-circle, 2°-diameter white circle, and 9°-diameter white circle conditions). Because there were only three Gains, we plotted the average corrected diffusion constants for perceived motion (cD_{PM}) as a function of the average diffusion constants for world motion (D_{WM}). If the subjects perceived the actual motion of the stimulus in the world, then the data points would lie along the 1:1 line. The small symbols represent each subject's average perceptual match for Gain -1.5 stimuli (blue open symbols), Gain 0 stimuli (yellow filled symbols), and Gain +1.5 stimuli (green filled

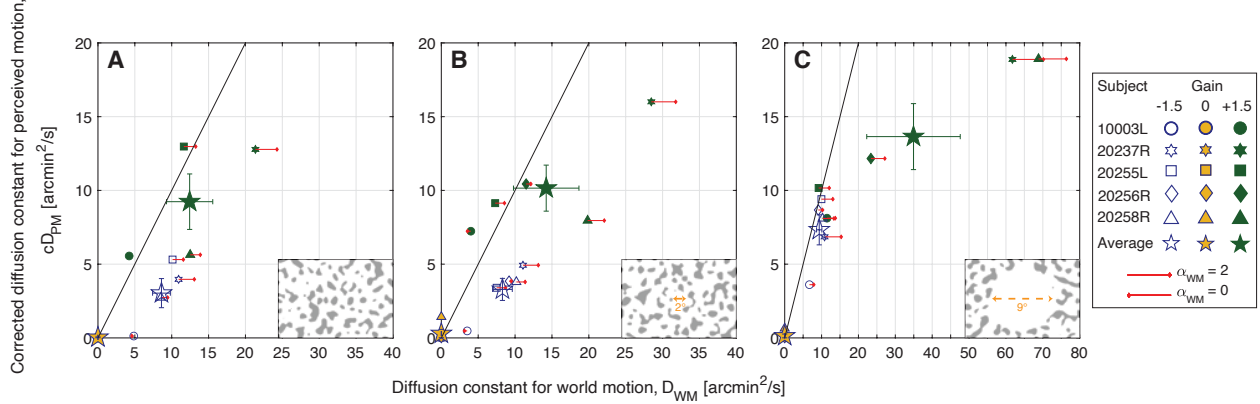


Figure 3.4: Experiment 2: Average corrected diffusion constants for perceived motion (cD_{PM}) versus diffusion constants for world motion (D_{WM}) from five subjects. Experiments were tested under three background conditions: The patterns extended over the full 17° field of view (A), or surrounded a 2° -diameter white circular opening (B), or surrounded a 9° -diameter white circular opening (C). Background conditions are indicated by labels on the *Lower Right* corner of each graph. Note that subject 20256R was not tested under the no-white-circle condition. The small symbols represent each subject's average perceptual match for Gain -1.5 stimuli (blue open symbols), Gain 0 stimuli (yellow filled symbols), and Gain $+1.5$ stimuli (green filled symbols). The large stars are the group averages with SE of the mean bars. The red arrows show the extent to which the eye motion, and consequent retina contingent stimulus' world motion (α_{WM}), deviated from Brownian. Arrows pointing *Right* indicate persistence ($\alpha_{WM} > 1$), arrows pointing *Left* indicate antipersistence ($\alpha_{WM} < 1$), and no arrow means that the motion was Brownian ($\alpha_{WM} = 1 \pm 0.02$). Longer arrows correspond to higher deviations from Brownian motion. The arrow length in the legend indicates pure persistence ($\alpha_{WM} = 2$, straight line trajectory at constant velocity) if pointing *Right* or pure antipersistence ($\alpha_{WM} = 0$, oscillatory motion) if pointing *Left*.

symbols). The large stars are the group averages with SE of the mean bars. The red arrows show the extent to which the eye motion, and consequent retina contingent stimulus' world motion (α_{WM}), deviated from Brownian. Arrows pointing *Right* indicate persistence ($\alpha_{WM} > 1$), arrows pointing *Left* indicate antipersistence ($\alpha_{WM} < 1$), and no arrow means that the motion was Brownian ($\alpha_{WM} = 1 \pm 0.02$). We did not show red arrows for the Gain 0 stimuli because motion statistics do not apply to world-fixed stimuli. As discussed in Chapter 2 [17], the presence of persistent eye motion generally gives rise to relatively higher values of the D_{WM} and relatively lower values of the diffusion constant of the random walk at the perceived match (D_{PM}). As a result, subjects with higher degrees of persistence tend to plot below the 1:1 line. Note that subject 20256R was not tested under the no-white-circle condition. Fig. 3.10 of Appendix 1 reports individual trial distributions of the matches for all subjects, and Fig. 3.11 of Appendix 1 reports the standard deviation of stimulus delivery

error distributions for all subjects.

The Illusion of Relative Stability Depends on the Extent of Retinal Image Background Content.

The illusion of relative stability persisted when the retinal image background content extended into – and even overlapped with – the retina-contingent stimulus. There was no statistically significant difference in perceived motion of Gain -1.5 stimuli between the no-white-circle and 2° -diameter white circle conditions (Fig. 3.4 *A* and *B*). For both backgrounds, Gain $+1.5$ stimuli were perceived to have more motion than Gain -1.5 stimuli ($P = 0.036$ for no-white-circle condition and $P = 0.037$ for 2° -diameter white circle condition, post hoc Tukey–Kramer). This is surprising considering that, under the no-white-circle condition, the stimulus in many instances would have crossed from dark to light background regions while the matches were being made.

On the other hand, subjects perceived significantly higher magnitudes of motion of Gain -1.5 stimuli when the retinal image background content was further displaced (the 9° -diameter white circle condition shown in Fig. 3.4*C*) from the retina-contingent stimulus ($P = 0.010$ compared to the no-white-circle condition and $P = 0.043$ compared to the 2° -diameter white circle condition, post hoc Tukey–Kramer). By spatially offsetting the background content $\sim 4^\circ$ from the stimuli, subjects perceived significantly higher magnitudes of motion of Gain -1.5 stimuli and perceptually underestimated the motion of Gain $+1.5$ stimuli (Fig. 3.4*C*), results that lean towards those tested in a Ganzfeld reported in Chapter 2 [17].

For Gain $+1.5$ stimuli, perceived motions were not significantly different between any background conditions (Fig. 3.4 *A* – *C*).

As an additional check, we performed the repeated-measures ANOVA and post hoc Tukey–Kramer tests using the original, uncorrected diffusion constants for perceived motion (D_{PM}) for all Gains and background conditions from Experiment 2 and these trends held.

Additional Analyses: Effect of Gain on Eye Motion Statistics.

Fig. 3.5 plots the average diffusion constants for eye motion (D_{EM}) and average α for eye motion (α_{EM}) for all subjects as a function of the Gains tested in Experiments 1 and 2. Within the violins [8], the central white circles represent the median and the dark gray bars represent the interquartile range. The surrounding intervals are the density traces [34].

Experiment 1.

Undergoing the same eye motion, increasing the magnitude of the Gain gives rise to higher magnitudes of the stimulus’ world motion. Therefore, we computed the ratio [average corrected diffusion constant for perceived motion]/[average diffusion constant for world motion],

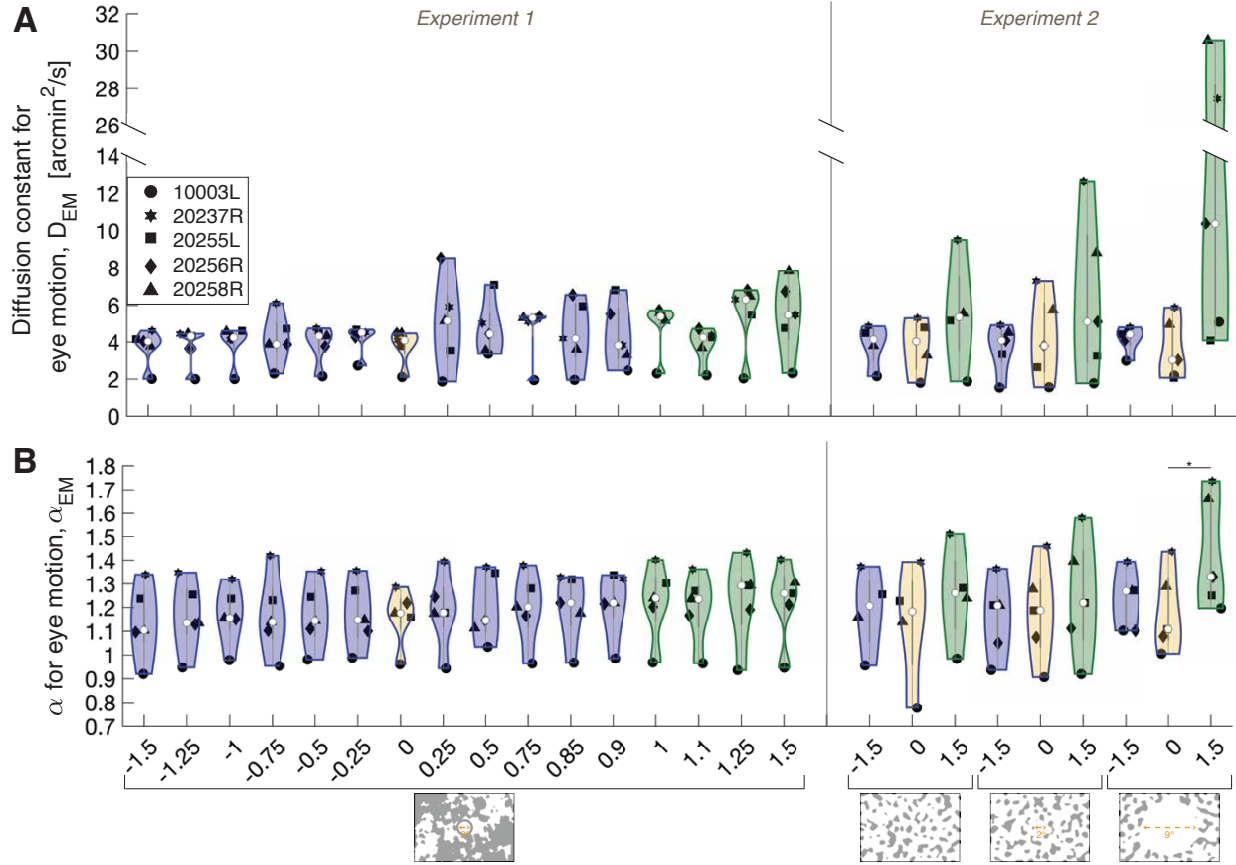


Figure 3.5: Violin plots showing the distribution of the (A) diffusion constant for eye motion, D_{EM} and (B) α for eye motion, α_{EM} as a function of the Gains from Experiments 1 and 2. Background conditions are indicated by labels beneath the graph. The violins outlined in blue (including the yellow-filled violin which labels the world-fixed stimulus) indicate the Gains where the stimulus' motion across the retina is in a direction that is directly opposite to eye motion. The violins outlined in green indicate the Gains where the stimulus' motion across the retina is in the same direction as eye motion. Within each violin, the central white circles represent the median and the dark gray bars represent the interquartile range. The surrounding intervals are the density traces. Each black point represents one subject and is the (A) average D_{EM} or (B) average α_{EM} across their trials for each Gain. The asterisk indicates statistical significance ($P < 0.05$) from a post hoc Tukey-Kramer test following a two-factor repeated-measures ANOVA.

or cD_{PM}/D_{WM} , to account for the world motion. We were motivated to ensure that Gain conditions did not impact the eye motion statistics, in particular the diffusion constant for eye motion, D_{EM} (Fig. 3.5A, Experiment 1) and α for eye motion, α_{EM} (Fig. 3.5B, Experiment 1). We found no significant difference between D_{EM} for Gains $< +1$ compared to D_{EM} for Gains $\geq +1$ ($P = 0.092$, Paired t-test). We found no significant difference between α_{EM} for Gains $< +1$ compared to α_{EM} for Gains $\geq +1$ ($P = 0.12$, Paired t-test).

Experiment 2.

A repeated measures ANOVA revealed no significant effect of Gain or background condition on D_{EM} ($P = 0.11$ and $P = 0.085$, respectively), however the interaction of Gain and background had a significant effect on D_{EM} ($P = 0.034$). A post hoc Tukey Kramer showed no significant differences between pairwise comparisons of D_{EM} (Fig. 3.5A, Experiment 2). This is likely due to small effect sizes between conditions which are not robust to the post hoc correction, given the current sample size ($n = 5$ subjects).

Additionally, a repeated measures ANOVA revealed a significant effect of Gain on α_{EM} ($P = 0.030$) but no significant effect of background condition on α_{EM} ($P = 0.094$). The interaction of Gain and background had a significant effect on α_{EM} ($P = 0.018$). Under the 9°-diameter white circle condition, the α_{EM} of Gain +1.5 stimuli were significantly higher than those of Gain 0 stimuli (Fig. 3.5B, Experiment 2).

Thus, the perceived motion (cD_{PM}) cannot be explained by changes in eye motion statistics, D_{EM} and α_{EM} , across Gain conditions. Offsetting the background content and turning off the fixation cross (9°-diameter white circle condition) can explain the higher D_{EM} and α_{EM} (Fig. 3.5 A and B, Experiment 2), which is consistent with a previous report [17].

3.5 Discussion

We demonstrate that perception of moving objects during fixational drift is discontinuous, governed by the direction those objects move with respect to eye motion. Our results build on previous studies [5, 17] and show that the direction that objects move with respect to eye motion is a critical parameter that governs an exception to our ability to detect relative motion.

Two Paradoxes in Motion Perception During Drift.

The human visual system relies on paradoxical methods to veridically perceive stable and moving objects.

Paradox 1: To perceive world-fixed objects in high resolution, the eye attempts to stabilize images-of-interest onto the fovea [25, 14]; yet, paradoxically, if the eye achieves perfect stability, the image will quickly fade from view [19, 69]. The eye therefore is in constant motion, and the human visual system evolved to discount the image motion due to eye motion, and even leverages its motion to improve spatial vision [68, 76].

Paradox 2: The visual system relies on world-fixed frames of reference to properly detect moving objects in the world [42]. However, the same frames of reference serve as retinal image background content to perceptually stabilize images that move in a direction consistent with retinal slip giving rise to the illusion of relative stability [17].

Where in the Visual Pathway Does the Illusion Take Place?

As discussed in Chapter 2 [17], the mechanisms underlying the illusion of relative stability at the earliest stages may rely on signals from the directionally sensitive retinal ganglion cells (DSRGCs) whose existence in primate have been recently reported [85]. Of course, the information from these cells could only be used to inform about eye motion; the percept could only be rendered after processing in higher cortical areas. A functional, circuit-level hypothesis has been proposed to explain how the behavior reported here and in previous papers might arise [4].

While the exact mechanisms remain unknown, the current study adds three important factors to consider: First, the illusion persists for Gains between 0 and +1, where the retinal image slip is consistent with, but less than, the eye's motion (Fig. 3.3). Second, the illusion is so profound that it persists even when the retinal image background content overlaps entirely with the retina-contingent stimuli (Fig. 3.4A). Third, if the retinal image background content is too far from the retina-contingent stimuli, then the effect diminishes (Fig. 3.4C), suggesting that the effect might not be a true discontinuity, but rather a graded response. To further elucidate possible mechanisms, the dependence on proximity to retinal image background content, and also the dependence on spatial frequency of that content can be explored. These remain parameters for future study.

Evaluating the Sharpness of the Discontinuity.

As mentioned above, the illusion of relative stability may not be a true discontinuity, but rather a graded response. We will review several reasons: First, if the retinal image background content is too far from the retina-contingent stimuli, then the effect diminishes (Fig. 3.4C) suggesting that the magnitude of this effect is driven by proximity to retinal image background content. Second, if it were a true discontinuity, the perceived motion (diffusion constant for perceived motion, D_{PM}) for Gains $< +1$ would be close to zero, regardless of Gain magnitude. However, all subjects showed a slightly increasing perception of motion (higher D_{PM}) as the Gains approached +1 or increased in retinal slip (Fig. 3.7 in Appendix 1). Third, in our experiments, all motion was restricted in two dimensions to be always aligned with the eye motion, either in the same direction or opposite; orientations of motion in other directions not aligned with eye motion also show a more gradual transition [5].

Further, even after accounting for stimulus delivery errors by computing the corrected diffusion constant for perceived motion, cD_{PM} , the perceived motion of stimuli moving opposite to eye motion (Gains $< +1$) did not go down to zero for most subjects. All subjects perceived slightly increasing magnitudes of motion as the Gains approached +1 or increased

in retinal slip (Fig. 3.7 in Appendix 1). This suggests that the motion the subjects saw was not solely due to stimulus delivery errors. And this suggests that higher magnitudes of stimulus motion, compared to the magnitude of eye motion, serve to diminish the illusion, supporting that this is a graded response. This is illustrated in Fig. 3.3B, the ratios for Gains $< +1$ are well fit with a quadratic function. While the D_{PM} and cD_{PM} increased slightly with Gain magnitude for Gains $< +1$, it is important to note that the D_{PM} and cD_{PM} remained well below the magnitude of the stimulus' motion in the world (diffusion constant for world motion, D_{WM}).

Comparison with the Results in Chapter 2.

In Arathorn et al. [5] and D'Angelo et al. (2024) (Chapter 2) [17], under background-present conditions, stimuli moving in the same direction as eye motion (Gains $\geq +1$) appeared readily in motion. For Gains $\geq +1$, we would expect that the motion the subjects perceived would be equal to the motion of the stimuli in the world. Arathorn et al. [5] did not quantify the magnitude of eye motion or the retina contingent stimulus' world motion so we cannot make any claims on whether the subjects veridically perceived the world motion of the retina-contingent stimuli. But D'Angelo et al. (2024) [17] computed the diffusion constant and α of the eye motion (D_{EM} and α_{EM}) and retina-contingent stimulus' world motion (D_{WM} and α_{WM}); the same method is used in this study, so we can compare the two studies as shown in Fig. 3.13A in Appendix 2. Note that D'Angelo et al. (2024) [17] only tested three Gains while this current paper tested sixteen Gains, and we therefore could only compare the results for Gains -1.5 , 0 , and $+1.5$ under background-present conditions. The results are generally the same but the differences in the experimental parameters and possible consequences of those are discussed in Appendix 2.

In D'Angelo et al. (2024) [17], we report results from experiments under a Ganzfeld condition. In the current study, as a control, we did the same method-of-adjustment experiments under a Ganzfeld as well, and we found the same trends: that motion perceptions reversed in the Ganzfeld. Similar to D'Angelo et al. (2024) [17], α_{EM} was significantly higher under the Ganzfeld ($P < 0.001$, Paired t-test). Results from those experiments are included in Fig. 3.12 of Appendix 1.

Comparison with Similar Research.

The jitter after-effect (JAE) illusion provides the best support for a retinal-image-based signal that gives rise to perceptual stability during fixation [55]. The JAE is a phenomenon whereby adapting retinal regions to dynamic random noise gives rise to perceptions of "jittering motion" in nearby unadapted regions. They proposed a motion-based model in which the visual system estimates the lowest velocity region and subtracts this velocity from all points on the retina. Our work complements this proposed model with the added observation that the retina-derived signal also drives the illusion of relative stability reported here. They also investigated the spatial extent of the JAE and found that it declined as the adapting field

was separated from the test field, becoming nearly zero at gap-widths between 4 - 8° of visual angle [56]. While we did not test the separation between the background content and the test stimuli very finely, we found that the illusion of relative stability diminishes as the size of the uniform window increases, nearly disappearing when it is open to a 9° visual angle.

Causal Inference in Perception.

The discontinuity that leads to the illusion of relative stability may arise from a causal inference process where, before estimating the actual motion of the stimuli, the visual system must decide if a given object is part of the world-fixed background or a moving object. Therefore, the illusion is in line with the notion of a visual system that has evolved to discount images moving with amplified retinal slip, as they are more likely to be part of the world-fixed stimuli. Given that it is highly unlikely that any object would ever move with amplified retinal slip for an appreciable time relative to other retinal image background content in the visual scene, it makes sense that such motion should never contaminate our perception. A causal inference framework could be used to formalize and explain this process. Causal inference has been used to explain perceptual processing in a growing number of studies [79, 20, 1]. Future work could uncover a causal inference model in motion perception during drift.

3.6 Conclusions

We showed that during fixational drift, the direction an object moves with respect to eye motion is a crucial parameter in giving rise to perceptions of stability and motion. Images moving opposite to eye motion, in a direction consistent with retinal slip, were perceived as relatively stable while the motion of images moving in the same direction was readily detected. This held even for stimuli that were slipping opposite to eye motion but with a smaller magnitude across the retina. We determined that this misperception persists even if the image moves on top of or close to retinal image background content – which is surprising and paradoxical given how this same content is used as a frame of reference to detect relative motion of images moving in any other direction with respect to eye motion.

3.7 Appendix 1

Linear and Nonlinear Fits.

For the data plotted on Figure 3.3B, we tested multiple breakpoints ranging from Gain -0.75 to $+1.1$, and performed independent fits to each side of the breakpoint, where x represents the Gain and y_i represents the [average corrected diffusion constant for perceived motion]/[average diffusion constant for world motion], or cD_{PM}/D_{WM} .

We tested independent, single-parameter linear fits on either side of the break point.

$$y_i = \begin{cases} a_1 & \text{if } x < \text{breakpoint} \\ a_2 & \text{if } x \geq \text{breakpoint} \end{cases} \quad (3.1)$$

We tested independent, two-parameter linear fits in slope-intercept form on either side of the breakpoint.

$$y_i = \begin{cases} a_1x + b_1 & \text{if } x < \text{breakpoint} \\ a_2x + b_2 & \text{if } x \geq \text{breakpoint} \end{cases} \quad (3.2)$$

We tested a quadratic fit to the left of the breakpoint and a single-parameter linear fit to the right.

$$y_i = \begin{cases} a_1x^2 + b_1x + c_1 & \text{if } x < \text{breakpoint} \\ a_2 & \text{if } x \geq \text{breakpoint} \end{cases} \quad (3.3)$$

If the discontinuity is weak, then the data would be best fit with a single function across all data points. We tested a quadratic, a cubic, and quartic function.

$$y_i = a_1x^2 + b_1x + c_1 \quad (\text{quadratic}) \quad (3.4)$$

$$y_i = a_1x^3 + b_1x^2 + c_1x + d_1 \quad (\text{cubic}) \quad (3.5)$$

$$y_i = a_1x^4 + b_1x^3 + c_1x^2 + d_1x + e_1 \quad (\text{quartic}) \quad (3.6)$$

The fit across all Gains, y_i , is expressed in Equation 3.1 – 3.6 and will be referred to as a “model”.

Akaike Information Criterion.

The Akaike information criterion (AIC) formula is expressed in Equation 3.7, where n is the sample size and $\hat{\sigma}^2$ is the average sum of the squared residuals or mean squared error (Equation 3.8). K is the number of regression parameters, including the intercept and variance [12]. As recommended by Burnham & Anderson [12], the AIC is added to a penalty term to reduce small-sample bias, shown in Equation 3.9.

$$AIC = n \log(\hat{\sigma}^2) + 2K \quad (3.7)$$

$$\hat{\sigma}^2 = \frac{1}{n} \sum_{i=1}^n (\hat{y}_i - y_i)^2 \quad (3.8)$$

$$AIC_c = AIC + \frac{2K(K+1)}{n-K-1} \quad (3.9)$$

AIC Interpretation: Computing Evidence Ratios.

Lower AIC_c values are considered “better”, given the models tested and the dataset. To estimate if the differences in AIC_c values are meaningful, we performed the following as suggested by Burnham & Anderson [12]:

1. Subtracted the lowest $AIC_{c_{min}}$ from each models’ AIC_{c_i} .

$$\Delta_i = AIC_{c_i} - AIC_{c_{min}} \quad (3.10)$$

2. Computed the likelihood of each model g_i given the same dataset x .

$$L(g_i|x) \propto e^{-\frac{1}{2}\Delta_i} \quad (3.11)$$

3. Computed “Akaike weights” w_i to determine the probability of each model g_i given R models tested.

$$w_i = \frac{L(g_i|x)}{\sum_{r=1}^R L(g_r|x)} \quad (3.12)$$

4. Computed “evidence ratios,” comparing each model’s Akaike weight w_i to the “best” model’s Akaike weight w_1 .

$$\text{Evidence ratio} = \frac{w_1}{w_i} \quad (3.13)$$

The w_i with the highest value is called w_1 . This means that there is strongest evidence that this is the “best” model, given R models tested. The evidence ratio is w_1/w_i , and therefore higher evidence ratios indicate stronger evidence for the “best” model. Lower evidence ratios indicate weaker support for the “best” model and suggests more uncertainty for model selection [12].

Control Experiment: Perceived Motion under Background-Absent (“Ganzfeld”) Conditions

As a control, we performed the same method-of-adjustment as in this current study, except that the stimuli were presented under background-absent (“Ganzfeld”) conditions. Using methods described in D’Angelo et al. (2024) (Chapter 2) [17], we set up a white paper with an aperture in front of the display permitting only the AOSLO and projector beams to enter the eye. We used the same aperture size as the one used in D’Angelo et al. (2024) [17]. LEDs were positioned between the subject and the paper to illuminate the paper. Due to its close proximity to the eye, the natural blur of the aperture in the paper rendered the transition between the display and luminance-matched paper invisible. Subjects performed the same matching procedure – fixating on the 680-nm cross and then attending to two circular stimuli. Subjects matched the motion of the left (random walk) stimulus to that of the right (retina-contingent) stimulus. To create a full Ganzfeld effect, we turned off the fixation cross during frames in which the two circular stimuli were presented. Without a fixation cross, eyes generally exhibit faster drift and larger corrective microsaccades [13].

To mitigate the effects of this increased retinal motion on the tracking accuracy, stimuli were presented for 750-ms. We measured the perceived motion of multiple retina-contingent stimuli with Gains ranging from -1.5 to $+1.5$ in increments of 0.25 . A total of thirteen Gains were tested and the subjects performed three trials per Gain (except for 20237R and 20255L, who only performed two trials of Gain $+0.75$; 20256R who only performed two trials of Gain -0.75 ; and 20258R who only performed two trials of Gain -1.5). Results from five subjects are shown in Fig. 3.12.

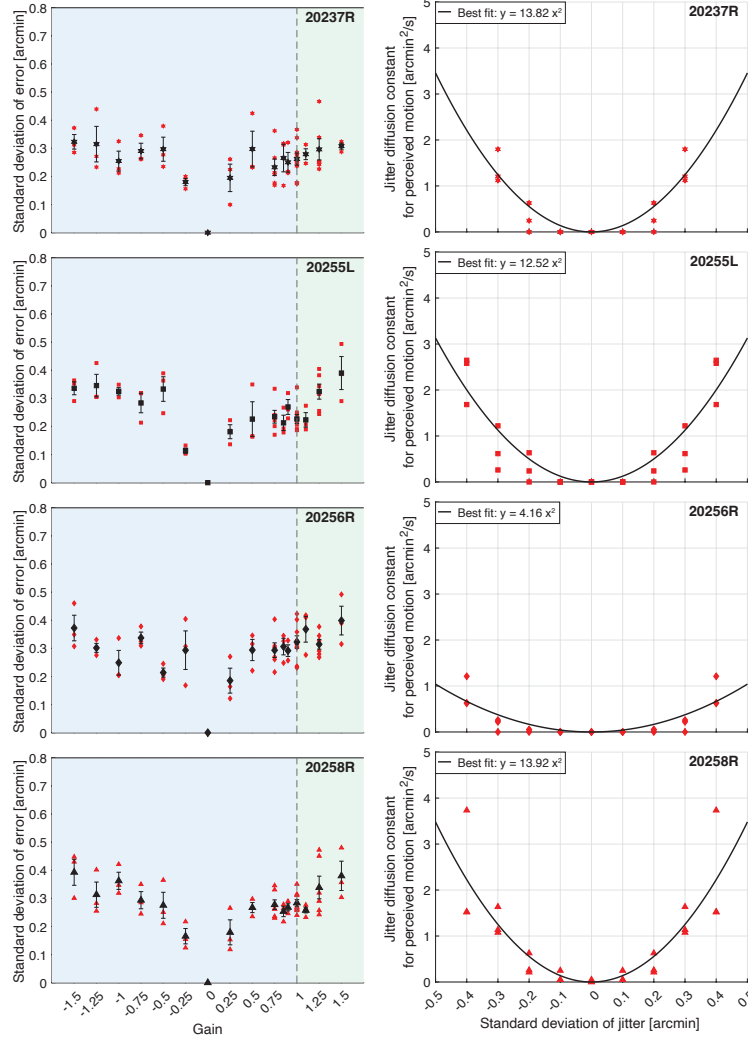
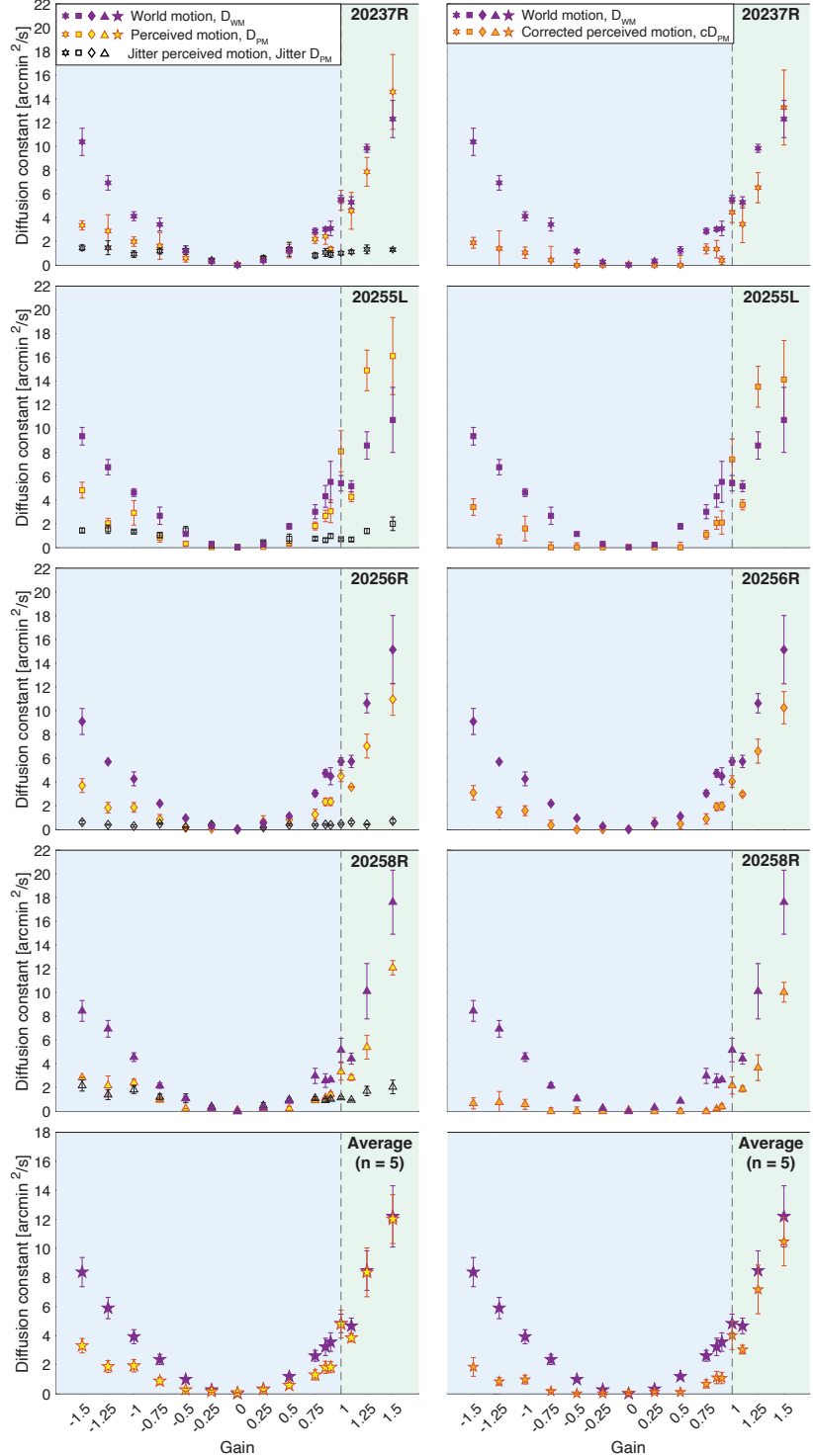


Figure 3.6: Experiment 1: Stimulus delivery error analysis from four subjects. The blue region of the graphs indicates the Gains where the stimulus' motion across the retina is in a direction that is directly opposite to eye motion. The green region indicates the Gains where the stimulus' motion across the retina is in the same direction as eye motion. (*Left Column*) The magnitude of stimulus delivery error for each Gain. For each trial, we computed the distances in x and y between the ideal retina-contingent stimulus motion trace and the measured retina-contingent stimulus motion trace. The red points indicate the standard deviation of error from one trial – this is the standard deviation across the distances in x and y from all frames from all videos within a single trial. The black points indicate the average standard deviation of error across all trials, with SE of the mean bars. (*Right Column*) Jitter diffusion constants for perceived motion, $Jitter D_{PM}$, plotted as a function of the standard deviation which was used to generate the jitter stimulus. Each red point represents one trial and was reflected across the y-axis. The black curve is a best-fit quadratic function which is anchored at 0 arcmin²/s. Note that because subject 20237R's average standard deviations of error were below 0.4 arcmin, we did not test this subject with a 0.4 arcmin standard deviation of jitter.

Figure 3.7: Experiment 1: Diffusion constants plotted as a function of the sixteen Gains. The blue region of the graphs indicates the Gains where the stimulus' motion across the retina is in a direction that is directly opposite to eye motion. The green region indicates the Gains where the stimulus' motion across the retina is in the same direction as eye motion. The top four rows show individual results from four subjects and the bottom row shows the averages across the five subjects, including 10003L whose data was shown in Fig. 3.2 *C* and *D*. Purple points indicate average diffusion constants for world motion, D_{WM} , with SE of the mean bars. (Left Column) Yellow points indicate average diffusion constants for perceived motion, D_{PM} , with SE of the mean bars. Black-hollow points indicate average *Jitter* D_{PM} with SE of the mean bars, given the standard deviation of error in Fig. 3.6. (Right Column) Orange points indicate average corrected diffusion constants for perceived motion, cD_{PM} , with SE of the mean bars. $cD_{PM} = D_{PM} - \text{Jitter } D_{PM}$.



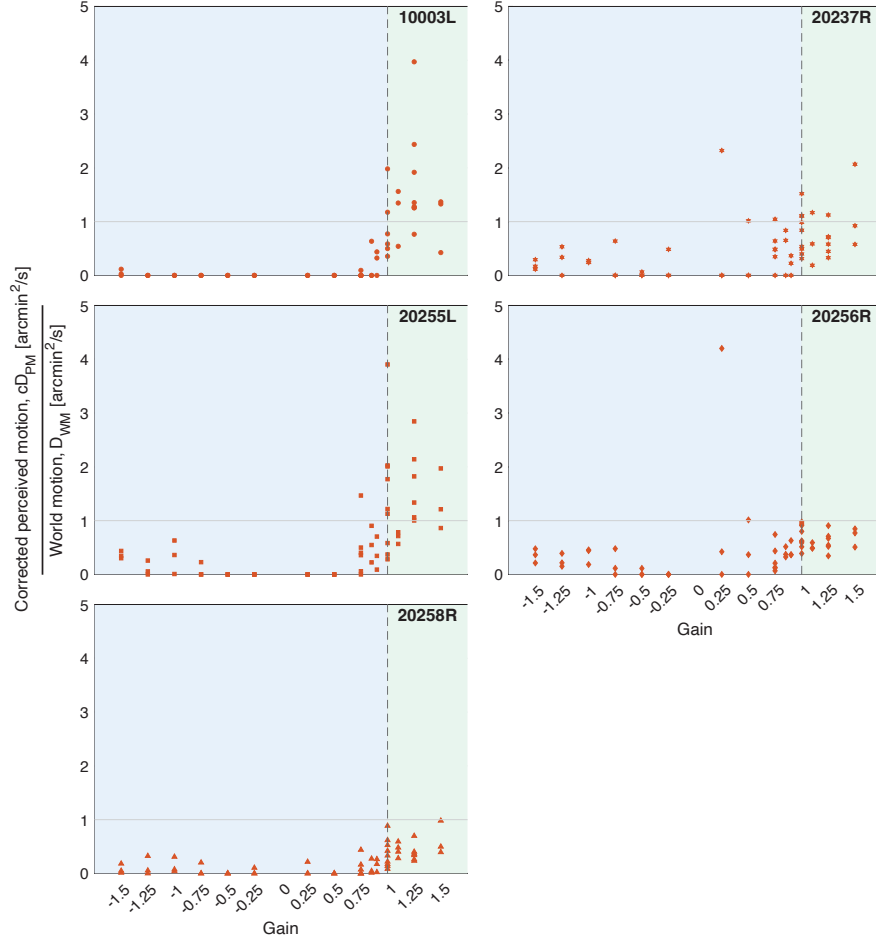


Figure 3.8: Experiment 1: Individual trial distribution of [average corrected diffusion constant for perceived motion]/[average diffusion constant for world motion], or cD_{PM}/D_{WM} , from five subjects as a function of the Gains. The blue region of the graphs indicates the Gains where the stimulus' motion across the retina is in a direction that is directly opposite to eye motion. The green region indicates the Gains where the stimulus' motion across the retina is in the same direction as eye motion. Each point represents one trial. Note that ratios for Gain 0 were removed.

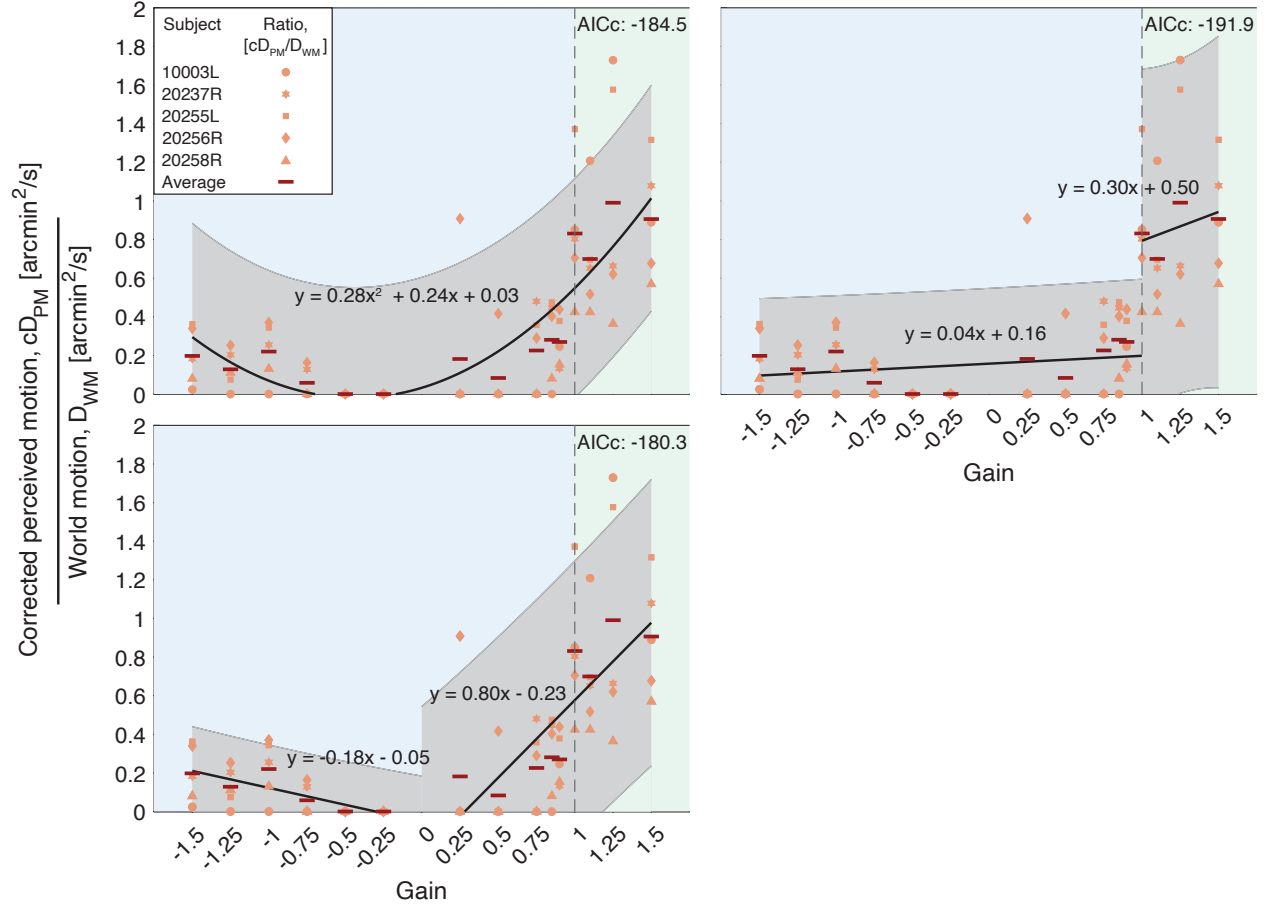


Figure 3.9: Experiment 1: Examples of linear and non-linear fits to the average ratios from five subjects. The blue region of the graphs indicates the Gains where the stimulus' motion across the retina is in a direction that is directly opposite to eye motion. The green region indicates the Gains where the stimulus' motion across the retina is in the same direction as eye motion. Each point represents one subject and is the [average corrected diffusion constant for perceived motion]/[average diffusion constant for world motion], or cD_{PM}/D_{WM} . The dark red bars indicate the average ratio across the five subjects. Note that ratios for Gain 0 were removed. The gray intervals indicate the 95% confidence bounds of the fits. The corrected Akaike information criterion, AIC_c , values are labeled on the *Top Right* corner of each graph. (*Top Panel*) A single quadratic fit across all points. (*Middle Panel*) Two independent, two-parameter lines in slope-intercept form on either side of a breakpoint at Gain 0. (*Bottom Panel*) Two independent, two-parameter lines in slope-intercept form on either side of a breakpoint at Gain +1.

Table 3.1: Evaluation of different fits to the [average **corrected** diffusion constant for perceived motion]/[average diffusion constant for world motion], or cD_{PM}/D_{WM} . Example fits are shown in Fig. 3.3B and Fig. 3.9 where x represents the Gain and y_i represents the cD_{PM}/D_{WM} . We tested the following models (a) Quadratic, cubic, and quartic functions across all data points. (b) Independent, single-parameter linear fits on either side of the multiple breakpoints ranging from Gain -0.75 to $+1.1$. (c) Independent two-parameter linear fits in slope-intercept form on either side of the same breakpoints. (d) A quadratic curve to the left and a single-parameter linear fit to the right for the same range of breakpoints.

One Continuous Fit						
Fit	AICc	Δ AICc	Likelihood	w	evidenceRatio	
Quadratic	-184.50	11.01	4.08E-03	2.24E-03		245.39
Cubic	-183.68	11.83	2.70E-03	1.48E-03		370.17
Quartic	-183.59	11.91	2.59E-03	1.42E-03		385.68

Two Horizontal Lines on Either Side of a Breakpoint						
Breakpoint	AICc	Δ AICc	Likelihood	w	evidenceRatio	
-0.75	-129.64	65.86	4.99E-15	2.74E-15		2.01E+14
-0.5	-132.85	62.65	2.49E-14	1.36E-14		4.02E+13
-0.25	-138.44	57.06	4.06E-13	2.23E-13		2.46E+12
0	-146.28	49.22	2.05E-11	1.13E-11		4.88E+10
0.25	-146.28	49.22	2.05E-11	1.13E-11		4.88E+10
0.5	-150.58	44.92	1.76E-10	9.65E-11		5.69E+09
0.75	-161.02	34.48	3.25E-08	1.78E-08		3.08E+07
0.85	-168.69	26.82	1.50E-06	8.25E-07		6.66E+05
0.9	-177.26	18.25	1.09E-04	5.99E-05		9.17E+03
1	-194.60	0.90	0.64	0.35		1.57
1.1	-168.01	27.50	1.07E-06	5.87E-07		9.36E+05

Two Lines in Slope-Intercept Form on Either Side of a Breakpoint						
Breakpoint	AICc	Δ AICc	Likelihood	w	evidenceRatio	
-0.75	-166.93	28.57	6.25E-07	3.43E-07		1.60E+06
-0.5	-171.49	24.01	6.11E-06	3.35E-06		1.64E+05
-0.25	-175.24	20.27	3.97E-05	2.18E-05		2.52E+04
0	-180.32	15.18	5.04E-04	2.77E-04		1.98E+03
0.25	-180.32	15.18	5.04E-04	2.77E-04		1.98E+03
0.5	-183.62	11.89	2.62E-03	1.44E-03		381.13
0.75	-183.81	11.69	2.89E-03	1.59E-03		346.08
0.85	-182.82	12.68	1.76E-03	9.67E-04		567.89
0.9	-183.29	12.22	2.22E-03	1.22E-03		449.44
1	-191.89	3.62	0.16	8.99E-02		6.11
1.1	-171.02	24.48	4.83E-06	2.65E-06		2.07E+05

A Quadratic Curve and a Horizontal Line on Either Side of a Breakpoint						
Breakpoint	AICc	Δ AICc	Likelihood	w	evidenceRatio	
-0.75	-125.12	70.38	5.21E-16	2.86E-16		1.92E+15
-0.5	-128.44	67.07	2.73E-15	1.50E-15		3.66E+14
-0.25	-134.69	60.82	6.21E-14	3.41E-14		1.61E+13
0	-142.99	52.51	3.95E-12	2.17E-12		2.53E+11
0.25	-142.99	52.51	3.95E-12	2.17E-12		2.53E+11
0.5	-147.09	48.42	3.06E-11	1.68E-11		3.27E+10
0.75	-157.43	38.08	5.40E-09	2.96E-09		1.85E+08
0.85	-165.83	29.67	3.61E-07	1.98E-07		2.77E+06
0.9	-175.98	19.52	5.76E-05	3.16E-05		1.74E+04
1	-195.50	0	1	0.55		1
1.1	-182.21	13.29	1.30E-03	7.14E-04		768.72

One Continuous Fit						
Fit	AICc	Δ AICc	Likelihood	w	evidenceRatio	
Quadratic	-153.90	6.22	4.45E-02	2.14E-02		22.47
Cubic	-152.47	7.65	2.18E-02	1.05E-02		45.87
Quartic	-150.22	9.90	7.08E-03	3.41E-03		141.18

Two Horizontal Lines on Either Side of a Breakpoint						
Breakpoint	AICc	Δ AICc	Likelihood	w	evidenceRatio	
-0.75	-129.51	30.61	2.26E-07	1.09E-07		4.43E+06
-0.5	-133.26	26.86	1.47E-06	7.07E-07		6.80E+05
-0.25	-140.43	19.69	5.30E-05	2.55E-05		1.89E+04
0	-140.85	19.27	6.54E-05	3.14E-05		1.53E+04
0.25	-140.85	19.27	6.54E-05	3.14E-05		1.53E+04
0.5	-137.78	22.34	1.41E-05	6.76E-06		7.11E+04
0.75	-140.64	19.48	5.89E-05	2.83E-05		1.70E+04
0.85	-145.83	14.29	7.88E-04	3.79E-04		1.27E+03
0.9	-150.39	9.73	7.70E-03	3.70E-03		129.91
1	-160.12	0	1	0.48		1
1.1	-147.84	12.29	2.15E-03	1.03E-03		465.72

Two Lines in Slope-Intercept Form on Either Side of a Breakpoint						
Breakpoint	AICc	Δ AICc	Likelihood	w	evidenceRatio	
-0.75	-146.58	13.54	1.15E-03	5.51E-04		873.07
-0.5	-147.01	13.11	1.42E-03	6.85E-04		702.31
-0.25	-146.84	13.28	1.30E-03	6.27E-04		766.88
0	-147.77	12.36	2.07E-03	9.97E-04		482.13
0.25	-147.77	12.36	2.07E-03	9.97E-04		482.13
0.5	-152.65	7.47	2.39E-02	1.15E-02		41.88
0.75	-153.34	6.78	3.37E-02	1.62E-02		29.65
0.85	-153.02	7.10	2.87E-02	1.38E-02		34.82
0.9	-153.71	6.41	4.05E-02	1.95E-02		24.70
1	-158.57	1.55	0.46	0.22		2.17
1.1	-151.02	9.10	1.05E-02	5.07E-03		94.83

A Quadratic Curve and a Horizontal Line on Either Side of a Breakpoint						
Breakpoint	AICc	Δ AICc	Likelihood	w	evidenceRatio	
-0.75	-125.26	34.87	2.68E-08	1.29E-08		3.73E+07
-0.5	-128.60	31.52	1.43E-07	6.89E-08		6.98E+06
-0.25	-136.20	23.92	6.39E-06	3.07E-06		1.57E+05
0	-136.71	23.41	8.25E-06	3.97E-06		1.21E+05
0.25	-136.71	23.41	8.25E-06	3.97E-06		1.21E+05
0.5	-136.84	23.28	8.81E-06	4.24E-06		1.14E+05
0.75	-138.33	21.79	1.85E-05	8.91E-06		5.40E+04
0.85	-142.93	17.19	1.85E-04	8.91E-05		5.40E+03
0.9	-148.03	12.09	2.36E-03	1.14E-03		422.92
1	-158.15	1.97	0.37	0.18		2.67
1.1	-151.37	8.75	1.26E-02	6.05E-03		79.44

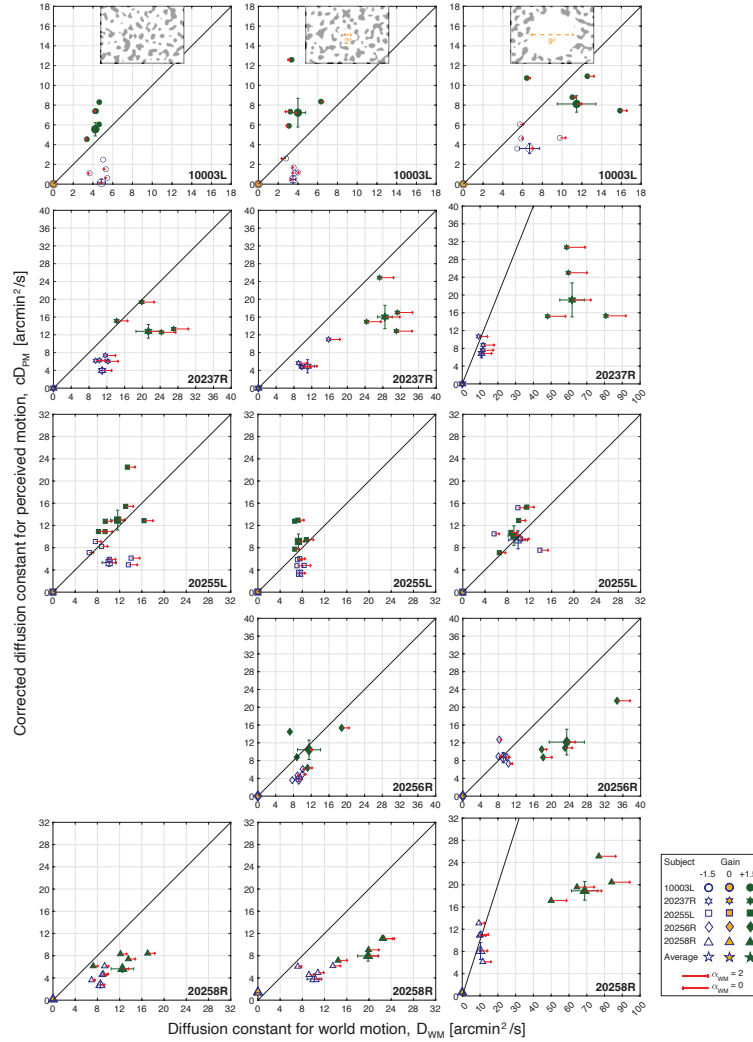


Figure 3.10: Experiment 2: Corrected diffusion constants for perceived motion (cD_{PM}) versus diffusion constants for world motion (D_{WM}) from five subjects. Experiments were tested under three background conditions: The patterns extended over the full 17° field of view (*Left Column*), or surrounded a 2° -diameter white circular opening (*Middle Column*), or surrounded a 9° -diameter white circular opening (*Right Column*). Background conditions are indicated by labels on the *Top* row. Each small symbol represents one trial: for Gain -1.5 stimuli (blue open symbols), Gain 0 stimuli (yellow filled symbols), and Gain $+1.5$ stimuli (green filled symbols). The large stars are the averages with SE of the mean bars. The y-axes are different to account for individual differences in eye motion and consequent retina-contingent stimulus' world motion (D_{WM}). The red arrows show the extent to which the eye motion, and consequent retina contingent stimulus' world motion (α_{WM}), deviated from Brownian. Arrows pointing *Right* indicate persistence ($\alpha_{WM} > 1$), arrows pointing *Left* indicate antipersistence ($\alpha_{WM} < 1$), and no arrow means that the motion was Brownian ($\alpha_{WM} = 1 \pm 0.02$). Longer arrows correspond to higher deviations from Brownian motion. The arrow length in the legend indicates pure persistence ($\alpha_{WM} = 2$, straight line trajectory at constant velocity) if pointing *Right* or pure antipersistence ($\alpha_{WM} = 0$, oscillatory motion) if pointing *Left*.

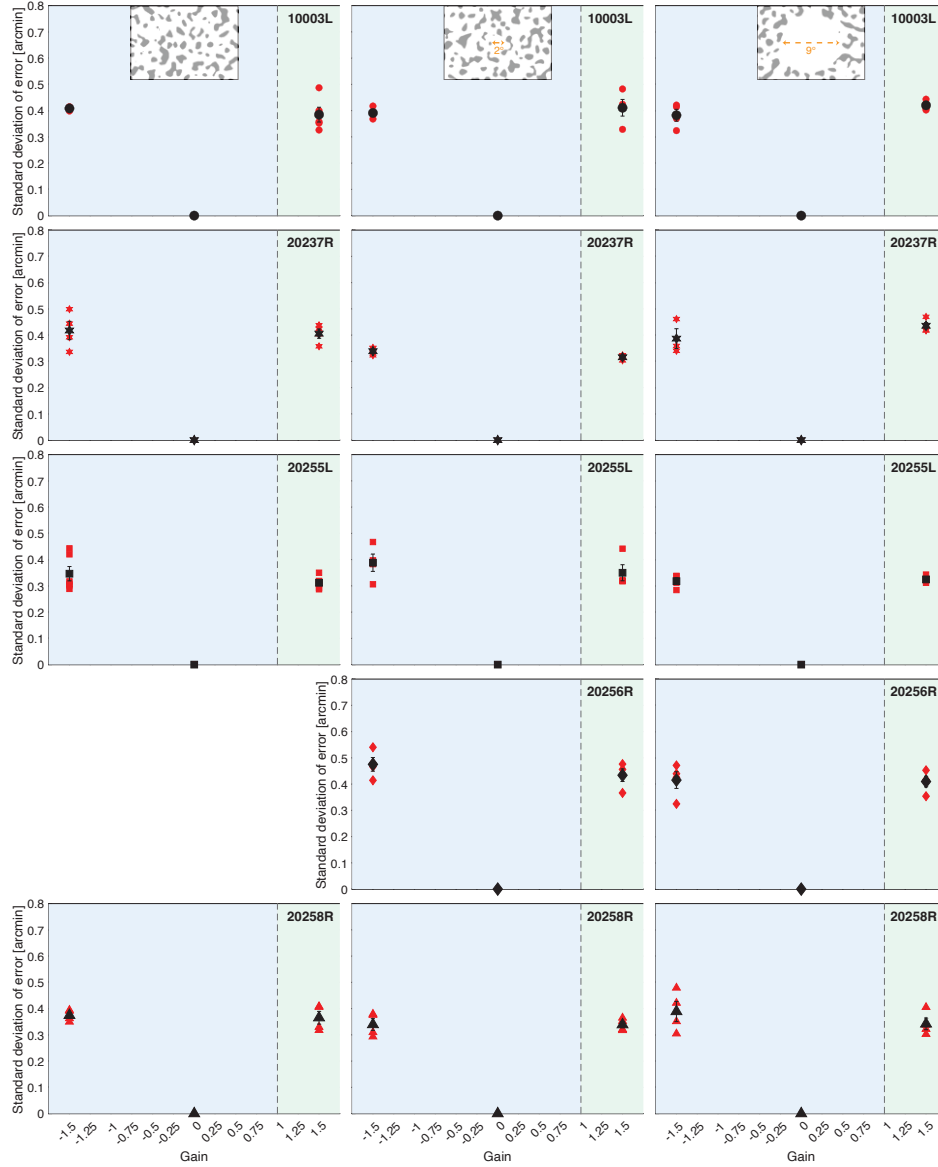


Figure 3.11: Experiment 2: The magnitude of stimulus delivery error for each Gain from five subjects. The blue region of the graphs indicates the Gains where the stimulus’ motion across the retina is in a direction that is directly opposite to eye motion. The green region indicates the Gains where the stimulus’ motion across the retina is in the same direction as eye motion. Experiments were tested under three background conditions: The patterns extended over the full 17° field of view (*Left Column*), or surrounded a 2°-diameter white circular opening (*Middle Column*), or surrounded a 9°-diameter white circular opening (*Right Column*). Background conditions are indicated by labels on the *Top* row. For each trial, we computed the distances in x and y between the ideal retina-contingent stimulus motion trace and the measured retina-contingent stimulus motion trace. The red points indicate the standard deviation of error from one trial – this is the standard deviation across the distances in x and y from all frames from all videos within a single trial. The black points indicate the average standard deviation of error across all trials, with SE of the mean bars.

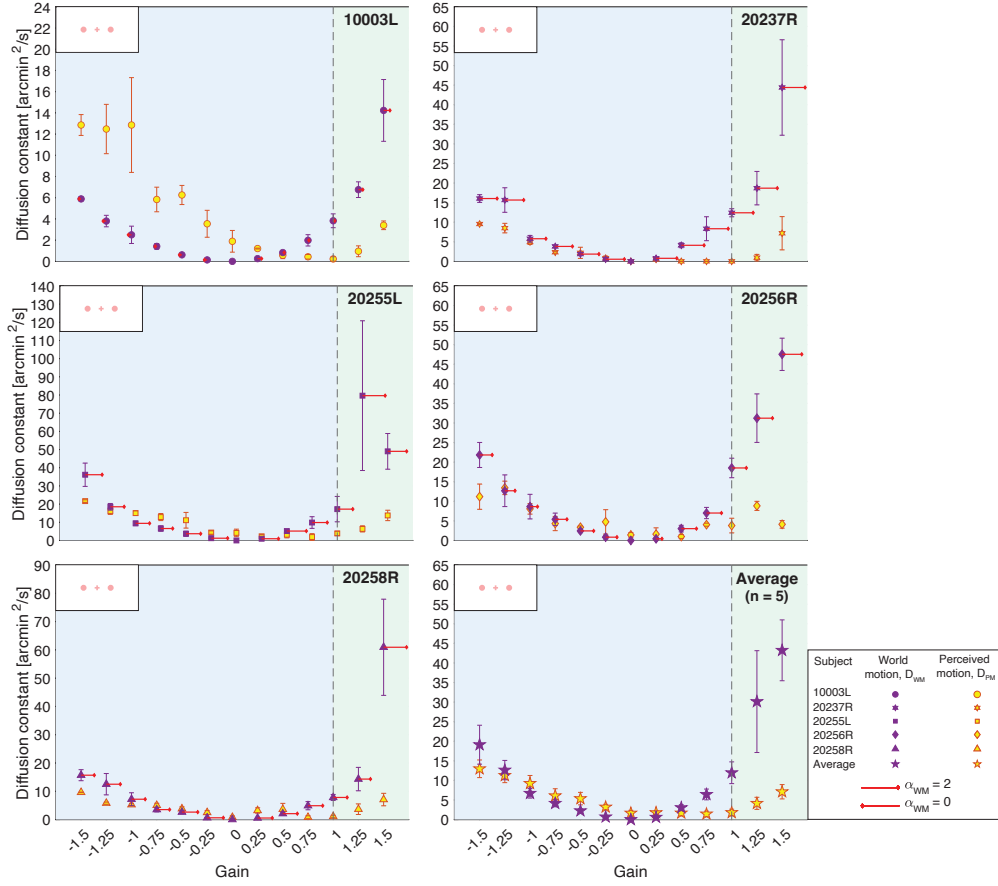


Figure 3.12: Control Experiment: Results from experiments tested under background-absent “Ganzfeld” conditions, indicated by labels on the *Top Left* corner of each graph. The blue region of the graphs indicates the Gains where the stimulus’ motion across the retina is in a direction that is directly opposite to eye motion. The green region indicates the Gains where the stimulus’ motion across the retina is in the same direction as eye motion. Note that the stimuli were presented for 750-ms for this condition. Average diffusion constants are plotted as a function of the Gains from five subjects. The orange symbols represent diffusion constants for perceived motion (D_{PM}) and the purple symbols represent diffusion constants for world motion (D_{WM}). (Note that the D_{PM} are the original, uncorrected values.) The y-axes are different to account for individual differences in eye motion and consequent retina-contingent stimulus’ world motion (D_{WM}). Each symbol is the respective average across all trials, with SE of the mean bars. The *Bottom Right* graph shows the averages across the five subjects, with SE of the mean bars. The red arrows show the extent to which the eye motion, and consequent retina-contingent stimulus’ world motion (α_{WM}), deviated from Brownian. Arrows pointing *Right* indicate persistence ($\alpha_{WM} > 1$), arrows pointing *Left* indicate antipersistence ($\alpha_{WM} < 1$), and no arrow means that the motion was Brownian ($\alpha_{WM} = 1 \pm 0.02$). Longer arrows correspond to higher deviations from Brownian motion. The arrow length in the legend indicates pure persistence ($\alpha_{WM} = 2$, straight line trajectory at constant velocity) if pointing *Right* or pure antipersistence ($\alpha_{WM} = 0$, oscillatory motion) if pointing *Left*.

3.8 Appendix 2: Comparison with the Results in Chapter 2

In Arathorn et al. [5] and D’Angelo et al. (2024) (Chapter 2) [17], under background-present conditions, stimuli moving in the same direction as eye motion (Gains $\geq +1$) appeared readily in motion. For Gains $\geq +1$, we would expect that the motion the subjects perceived would be equal to the motion of the stimuli in the world. Arathorn et al. [5] did not quantify the magnitude of eye motion or the retina contingent stimulus’ world motion so we cannot make any claims on whether the subjects veridically perceived the world motion of the retina-contingent stimuli. But D’Angelo et al. (2024) [17] computed the diffusion constant and α of the eye motion (D_{EM} and α_{EM}) and retina-contingent stimulus’ world motion (D_{WM} and α_{WM}); the same method is used in this study, so we can compare the two studies, shown in Fig. 3.13A.

Fig. 3.13A plots the average diffusion constants for perceived motion (D_{PM}) versus diffusion constants for world motion (D_{WM}). (Note that the D_{PM} are the original, uncorrected values.) Results were collected from five subjects for this current paper and six subjects for D’Angelo et al. (2024), indicated by light and dark colors, respectively. For both studies, experiments were tested under background-present conditions: the background was filled with a blurred and binarized 1/f noise pattern with a 2°-diameter central white circle with a surrounding black ring that overlaid the 680-nm stimuli, shown in Fig. 3.1A. The small symbols represent each subject’s average perceptual match for Gain -1.5 stimuli (light- and dark-blue open symbols), Gain 0 stimuli (light- and dark-yellow filled symbols), and Gain $+1.5$ stimuli (light- and dark-green filled symbols). The 1:1 indicates veridical perception of motion.

In this study, for Gains $+1.5$ (light green data points in Fig. 3.13A), three subjects overestimated the motion (10003L, 20237R, and 20255L) and two subjects underestimated the motion (20256R and 20258R). As a result, the average perceived motion across subjects (large light-green star in Fig. 3.13A) was approximately equal to the world motion of the stimuli. In D’Angelo et al. (2024) [17], for Gains $+1.5$ (dark green data points in Fig. 3.13A), five subjects underestimated the motion and only one subject (10003L) reported motion that was similar to the world motion. As a result, the average perceived motion across subjects (large dark-green star in Fig. 3.13A) was below the world motion of the stimuli.

We will discuss three factors that could contribute to this:

1. Inter- and intra-subject variability.

Participants were different between studies. We may have by random chance recruited subjects who were naturally biased to underestimate motion in D’Angelo et al. (2024) [17] (inter-subject variability). It is important to mention that in each study, no specific criteria were given to the subjects to make the match, so the subjects who were recruited for both studies may have changed criteria between the studies (intra-subject variability). As shown in Fig. 3.13A, for Gain $+1.5$ stimuli, 10003L (circle) performed similarly between

both studies, but 20237R (hexagram) and 20256R (diamond) perceived more motion in this current paper compared to D’Angelo et al. (2024) [17].

2. Eccentricity.

We presented stimuli 0.43° away from the fovea in this study; however, stimuli were delivered 2° away from the fovea in D’Angelo et al. (2024) [17]. Motion perception thresholds have been shown to increase with eccentricity [9, 49]. Interestingly, the perceived motion of Gain -1.5 stimuli are also higher in this current paper (light- vs dark-blue in Fig. 3.13A).

3. α for world motion, α_{WM} .

We discussed in D’Angelo et al. (2024) [17] that a higher α leads to a higher diffusion constant (D), given the same average step length. (“Step length” refers to the standard deviation of the randomized step lengths within a trajectory). In other words, for a subject with persistent eye motion, the subsequent retina-contingent stimulus has a high α_{WM} and a higher diffusion constant compared to a trajectory with the same average step length but with an α equal to one. Since the subject always compares a Brownian random walk stimulus to their potentially highly persistent retina-contingent stimulus motions, this could lead to high diffusion constants for world motion (D_{WM}), leading to smaller D_{PM}/D_{WM} that convey underestimated values of motion perception. This was especially relevant in the Ganzfeld condition, where the α_{WM} ’s were as high as 1.7. (Note that an α of 2 is maximum persistence, a straight line trajectory at constant velocity.) Subjects expressed no frustration when asked to match a persistent trajectory to a Brownian trajectory. Reported in D’Angelo et al. (2024) [17], subjects perform poorly at discriminating a highly persistent motion (e.g. $1.3 < \alpha < 1.7$) with a high diffusion constant from a less persistent motion (e.g. $1 < \alpha < 1.3$) with a low diffusion constant.

But, under background-present conditions, the α_{WM} ’s are similar between D’Angelo et al. (2024) [17] and this current paper (indicated by red arrows in Figure 3.13A). α_{WM} cannot fully explain the motion perception differences between the two studies. We plotted the [average diffusion constant for perceived motion]/[average diffusion constant for world motion], or D_{PM}/D_{WM} , from Fig. 3.3B as a function of each subject’s α_{WM} , for four Gains: $+1$, $+1.1$, $+1.25$, and $+1.5$. The respective colors go from light to dark green, shown in Fig. 3.13B. Using the same procedure from D’Angelo et al. (2024) [17], we modeled how the ratios would vary with α_{WM} under a specific condition where the subject equated the mean square displacement (MSD) between the motion of the random walk stimulus over a specific time interval. In the model, the random walk stimulus’ α , which represents the α_{PM} , is equal to one (Brownian motion), while the retina-contingent stimulus’ α_{WM} ranges from antipersistent ($0.9 \leq \alpha_{WM} < 1$), to Brownian ($\alpha_{WM} = 1$), to persistent ($1 < \alpha_{WM} \leq 1.8$). By a least-squares procedure, we determined that a time interval of 28 frames best predicted the measured data. The model is represented by a solid curve in Fig. 3.13B.

In D'Angelo et al. (2024) [17], computing the MSD over a time interval of 2 frames best predicted the measured data. This analysis suggests that subjects make motion judgments for perifoveal stimuli over longer time intervals (14x longer) in this study, compared to stimuli presented at greater eccentricities. This could also be due to the stimuli being presented side-by-side instead of over intervals of time. Further work could evaluate each subjects' specific time interval over which they make motion judgments.

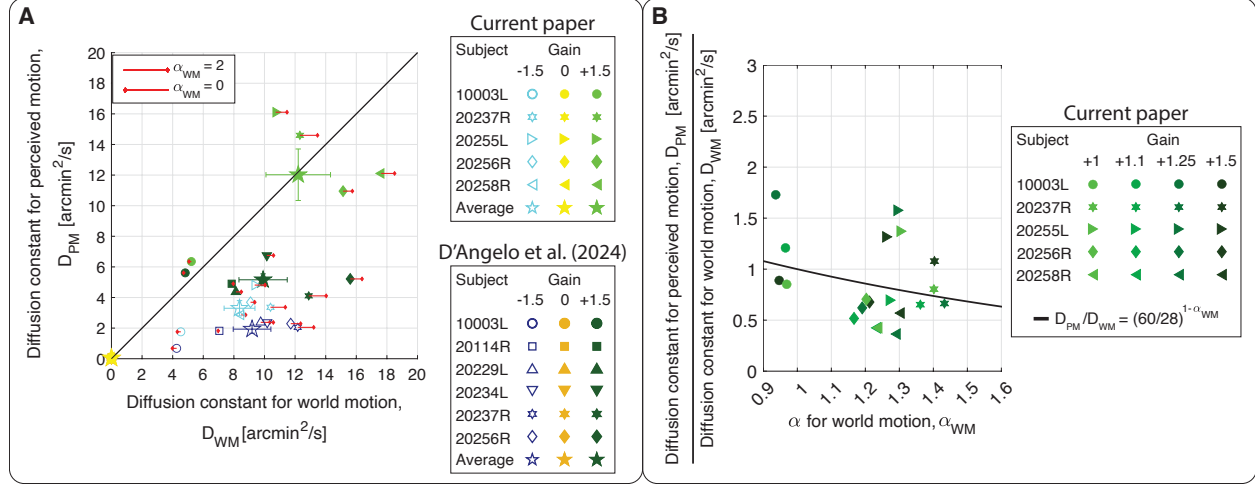


Figure 3.13: Comparing results from this paper (Chapter 3) [16] to D'Angelo et al., (2024) (Chapter 2) [17]. (A) Average diffusion constants for perceived motion (D_{PM}) versus diffusion constants for world motion (D_{WM}). (Note that the D_{PM} are the original, uncorrected values.) Results were collected from five subjects for this current paper and six subjects for D'Angelo et al. (2024), indicated by light and dark colors, respectively. All experiments were tested under background-present conditions. The small symbols represent each subject's average perceptual match for Gain -1.5 stimuli (light- and dark-blue open symbols), Gain 0 stimuli (light- and dark-yellow filled symbols), and Gain $+1.5$ stimuli (light- and dark-green filled symbols). The large stars are the group averages with SE of the mean bars. The red arrows show the extent to which the eye motion, and consequent retina-contingent stimulus' world motion (α_{WM}), deviated from Brownian. Arrows pointing *Right* indicate persistence ($\alpha_{WM} > 1$), arrows pointing *Left* indicate antipersistence ($\alpha_{WM} < 1$), and no arrow means that the motion was Brownian ($\alpha_{WM} = 1 \pm 0.02$). Longer arrows correspond to higher deviations from Brownian motion. The arrow length in the legend indicates pure persistence ($\alpha_{WM} = 2$, straight line trajectory at constant velocity) if pointing *Right* or pure antipersistence ($\alpha_{WM} = 0$, oscillatory motion) if pointing *Left*. (B) Computed ratios from five subjects plotted as a function of each subject's α for world motion, α_{WM} . The symbols represent each subject's [average diffusion constant for perceived motion]/[average diffusion constant for world motion], or D_{PM}/D_{WM} . (Note that the D_{PM} are the original, uncorrected values.) Data are from four Gains: $+1$, $+1.1$, $+1.25$, and $+1.5$, and the respective colors go from light to dark green. The black curve predicts the D_{PM}/D_{WM} versus α_{WM} , considering that the subject matched the mean squared displacements of the random walk stimulus with the retina-contingent stimulus over a time interval of 28 frames.

Acknowledgments

The authors thank Dr. Benjamin M. Chin for his helpful discussions. This research was supported by funding from National Institutes of Health Grants R01EY023591 (A.R.) and T32 EY007043 (J.C.D.), the Center for Innovation in Vision and Optics (civo.berkeley.edu) (J.C.D.), and a grant from the Minnie and Roseanna Turner Fund for Impaired Vision Research (J.C.D.).

Competing Interests.

P.T. and A.R. are co-inventors on US Patent #10130253, assigned to the University of California.

Author Contributions.

This paper was published in 2026. J.C.D., P.T., R.J.W., D.W.A., J.O.M., and A.R. designed research; J.C.D. and A.R. performed research; J.C.D. and A.R. analyzed data; P.T. and R.J.W. provided critical technical support; and J.C.D., D.W.A., J.O.M., and A.R. wrote the paper.

Citation for This Paper

D'Angelo, J. C., Tiruveedhula, P., Weber, R. J., Arathorn, D. W., Otero-Millan, J., & Roorda, A. (2026). A discontinuity in motion perception during fixational drift. *Journal of Vision*, 26(1), 2-2.

Chapter 4

Misperceptions of motion during smooth pursuit

4.1 Introduction

The studies presented in Chapters 2 and 3 quantified the perceived motion of images moving contingent to the retina during fixational drift. However, images would not naturally move in this manner for an appreciable amount of time; during fixation, the eye constantly changes direction as it traverses an approximately random trajectory [14, 16, 17, 24, 41, 51, 71]. Thus, an image moving in a direction consistent with retinal slip in one instance would quickly change directions on the retina as the eye ever-changes its direction of motion. Presenting a stimulus that only moves in a direction consistent with retinal slip during drift requires a real-time eye tracking system so that the image can be programmed to move with respect to eye motion.

But, an image can naturally slip in a direction consistent with retinal slip during smooth pursuit. For example, consider a hypothetical scenario in which two cars move along the horizon, with one ahead of the other. The leading car is moving 25 miles per hour (mph), while the trailing car is moving 20 mph. If you were to track the leading car and attend to the trailing car, the image of the trailing car would slip opposite to eye motion, slowly lagging further away from the leading car over time. Since the image of the trailing car is moving in a direction consistent with retinal slip, would it appear stable relative to the background? In this chapter, we investigate whether the “illusion of relative stability” extends to situations involving smooth pursuit.

When the eye tracks a moving target, the stationary background sweeps across the retina by a magnitude equal to the eye movements. Motion perception during smooth pursuit relies on combining retinal image motion signals with extraretinal signals that estimate the eye’s movements, however; compensation is imperfect. For example, errors in compensation give rise to illusions like the Filehne illusion, where a stationary background appears to move in the opposite direction of pursuit [26].

Prior Study Measuring Sensitivity to Retinal Slip During Smooth Pursuit.

Motion perception during smooth pursuit has also been shown to be affected by the direction of retinal slip. Turano & Heidenreich (1996) [83] tested whether speed discrimination thresholds change in a manner consistent with the pursuit-driven transformed retinal speed. According to Weber's law, just noticeable differences scale with the magnitude of the original stimulus [30]. Thus, it would make sense for the speed discrimination thresholds to increase as the speed of the stimulus, relative to the tracked target, increases.

In the task, the subjects pursued a vertical bar and attended to a sine-wave grating. They tested three conditions that varied the retinal slip of the grating image. The eye moved: 1) opposite to the grating (amplified retinal slip), 2) in the same direction as the grating but slower (the retinal image moved in advance of the eye), or 3) in the same direction as the grating but faster (the retinal image slipped opposite to the eye motion over time).

They found that when the eye moved opposite to the grating (condition 1) or in the same direction as the grating but slower (condition 2), speed discrimination thresholds changed in a manner consistent with the transformed retinal speed due to pursuit eye movements. For example, higher eye speeds moving in the opposite direction to the grating corresponded to higher speed discrimination thresholds.

However, when the eye moved in the same direction as the grating but faster (condition 3), the speed discrimination thresholds were surprisingly higher than what would be predicted by the retinal motion. When the image moved in a direction consistent with retinal slip, the subjects showed an unexpected low sensitivity to speed changes and the authors concluded that "some other factor is needed to account for this case". However, in the context of Chapters 2 and 3 and previous work [5], these results are not unexpected.

Current Study Measuring Motion Perception During Smooth Pursuit.

In this chapter, we investigate whether the "illusion of relative stability" for all images moving in a direction consistent with retinal slip persists during smooth pursuit. Consider the hypothetical scenario introduced at the beginning of the chapter, except that now there are three cars moving along the horizon, one after the other. The leading car is moving 30 mph, the middle car is moving 25 mph, and the trailing car is moving 20 mph. If you were to track the middle car and attend to the leading and trailing cars: in the world, both the leading and trailing cars would separate from the middle car at an equal rate of 5 mph. On the retina, the image of the trailing car would slip opposite to eye motion, in a direction consistent with retinal slip; while the image of the leading car would move ahead of eye motion. Thus, would the images appear to separate at unequal rates? Specifically, since the trailing car moves in a direction consistent with retinal slip, would it appear relatively stable, and thus appear to separate faster? We designed an experiment testing this scenario. Because the perceptual question was about the gap between the cars, we designed black bar

stimuli, that occupied the gap, which grew at different rates away from the pursuit target. The psychophysical question became, “which bar length was increasing faster, the left or right?”

4.2 Methods

Subjects.

Eleven subjects (2 experienced and 9 naive; 8 female and 3 male; ages 22-59 with an average age = 30.9 years) were recruited. Subjects provided informed consent to participate and had normal or corrected-to-normal vision. The experiment was approved by the Institutional Review Board at the University of California, Berkeley and adheres to the principles outlined in the Declaration of Helsinki.

Apparatus.

Subjects’ were positioned 66 cm away from a screen (Acer Predator Monitor, 120 Hz refresh rate, 54.5 x 30.5 cm, 1920 x 1080 pixels). Background patterns and stimulus presentation were programmed with MATLAB (MathWorks, Natick, MA, USA) using the Psychophysics Toolbox [11, 39, 62]. Subjects viewed the screen binocularly and a chin rest and temple pads were used to immobilize the head.

Eye Tracker and Calibration.

Eye motion was recorded using a custom-built binocular eye tracker running at 250 Hz (interpolated to 500 Hz). We used Open Iris [77] to perform corneal reflection pupil eye tracking (P-CR). Prior to the experiments, subjects performed a calibration viewing 13 saccade targets (0.5°-diameter circles) which were presented in a random order within a region spanning 20 x 5°. The calibration enabled us to translate the screen pixel values into degrees of visual angle.

Experimental Procedure.

The screen displayed a blurred and binarized 1/f noise pattern that changed after each presentation. This background was used to provide world-fixed retinal image background content, which had been shown in Chapters 2 and 3 to be necessary to give rise to the “illusion of relative stability”. A 25.2 x 1.4° white gap in the pattern extended horizontally across the center of the screen (Fig. 4.1A). Within this white gap, the pursuit target and stimuli appeared. The pursuit target was a 0.47°-diameter black circle with a central white cross (0.12° bar-width). The stimuli were black bars of initial size 1.76 x 0.70° which horizontally grew away from the target over time by an absolute rate ranging from 0.96°/s to 1.440°/s,

depending on the trial condition. The experiment sequence (Fig. 4.1B) for one trial went as follows:

- A pursuit target appeared 6° to the left or right from center and remained stationary for 0.5 seconds.
- The pursuit target began moving towards the center at $6^\circ/\text{s}$ for 1 second.
- While the pursuit target continued moving at $6^\circ/\text{s}$, two black bars, appeared on either side of the target and grew at different rates for 1 second.
- The bars faded away to white for the last 0.5 seconds.

After the trial, the subjects viewed a multicolored mosaic, adapted from the “wipeout” pattern used in previous works [28, 40], which was used to mask afterimages, ensuring that subjects made motion judgments instead of relying on positional cues (Fig. 4.1C). For the entirety of the trial, the subject was instructed to pursue the target and attend to the black bars on either side. After the trial, they responded, by button press, “which bar length was increasing faster, the left or right?” Their response initiated the next trial. The stimuli moved leftward in half of the trials; and rightward in the other half, in a pseudorandom order.

The subjects first started with a training block of 18 trials to practice performing pursuit eye movements and to become familiar with the task. The experiments were performed in a lit room.

Conditions.

We tested two conditions, varying the rate-of-growth of either the trailing bar or the leading bar. In the first condition, the trailing bar (reference) grew outward from the pursuit target at a rate of $-1.2^\circ/\text{s}$; while the leading bar (test) grew outward from the pursuit target at rates ranging from $0.96^\circ/\text{s}$ to $1.440^\circ/\text{s}$, in step sizes of 0.06° . Each of the nine rates were replicated eight times using a method of constant stimuli paradigm. In the second condition, the trailing bar (test) grew outward from the pursuit target at rates ranging from $-1.440^\circ/\text{s}$ to $-0.96^\circ/\text{s}$, in step sizes of 0.06° ; while the leading bar (reference) grew outward from the pursuit target at a rate of $1.2^\circ/\text{s}$. Each of the nine rates were replicated eight times. Note that the sign indicates the direction of growth relative to the pursuit target: positive indicates growth in the same direction as the pursuit target and negative indicates growth in the opposite direction. Across both conditions, we tested a total of 144 trials, presented in a pseudorandom order.

Control Experiment.

As a control, we used the exact same experimental procedure except that we turned off the pursuit target. This ensured that the onset time of the stimuli in the control experiment

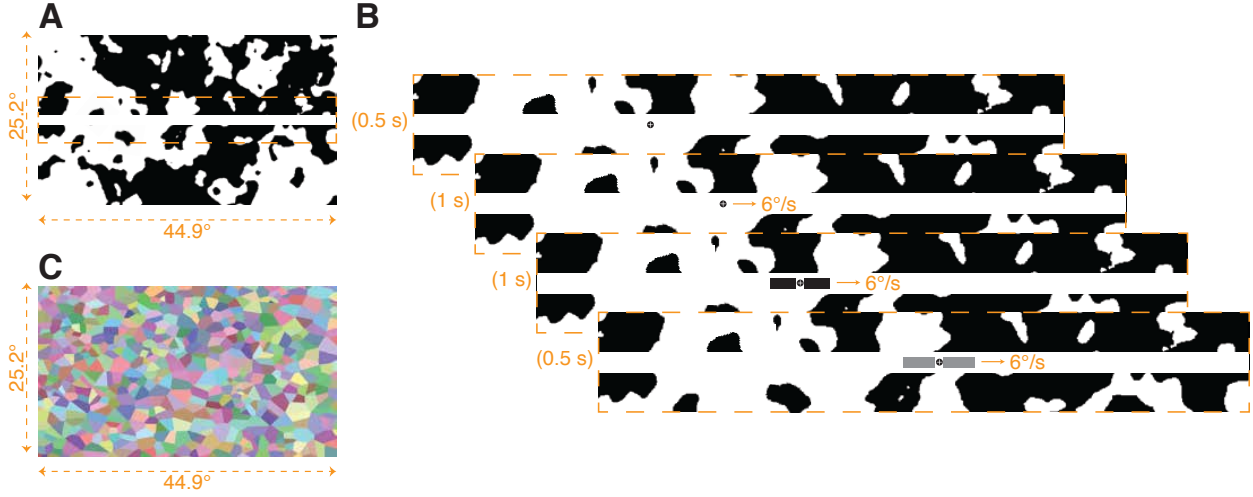


Figure 4.1: Display configuration. (A) The $44.9^\circ \times 25.2^\circ$ screen displayed a blurred and binarized $1/f$ noise pattern that changed after each presentation. A $25.2^\circ \times 1.4^\circ$ white gap extended horizontally across the center of the screen. Within this white gap, the pursuit target and stimuli appeared. (B) Experimental sequence for one trial: 1) A pursuit target appeared 6° to the left or right from center and remained stationary for 0.5 seconds; 2) The pursuit target began moving towards the center at $6^\circ/\text{s}$ for 1 second; 3) While the pursuit target continued moving at $6^\circ/\text{s}$, two black bars, appeared on either side of the target and grew at different rates for 1 second; 4) The bars faded away to white for the last 0.5 seconds. We used the exact same procedure for the control experiment, except the pursuit target was turned off. Note that the region dimensions are indicated by a orange border shown in A. (C) After the trial, the subjects viewed a multicolored mosaic which was used to mask afterimages.

equaled that in the pursuit experiment. The subject was allowed to move their eyes freely but was encouraged to move their eyes back-and-forth between the black bars to make their judgment. After the trial, they responded to the same question, “which bar length was increasing faster, the left or right?” By removing the pursuit eye motion, the trailing bar no longer slipped in a direction consistent with retinal slip. The pursuit and control experiments were collected in the same session with subjects 0213, 0232, 0241, and 0242 first doing the control experiment and subjects 0108, 0162, 0164, 0174, 0197, 0199, and 0240 first doing the pursuit experiment.

Saccade Filtering.

After the experiments, we recovered binocular eye traces for each trial. We analyzed only the left eye traces and restricted analyses to the one-second stimulus presentation window. For each trial, we used an algorithm designed by Engbert and Kliegl [23] to detect saccades;

detection is based on the standard deviation of eye velocity, with parameter $\lambda = 6$. This means that eye velocities greater than 6 standard deviations from the mean were classified as saccades.

For the pursuit experiment, we performed a series of filtering steps on the eye motion traces. This was necessary because saccades alter the way images move on the retina; in particular, horizontal backward saccades can change the direction of stimulus motion relative to eye motion, potentially disrupting the conditions we aimed to establish. Thus, we evaluated the saccade amplitude in the x-dimension. First, we did not consider the subject responses for all trials containing saccades with x-amplitudes greater than 1° . Next, we did not consider the subject responses for all trials that contained backward saccades in the x-dimension. For the control experiment, because subjects were permitted to move their eyes freely, all trials were included in the analysis.

Perceptual Data Analysis.

A logistic psychometric function was fit to the remaining data using the Palamedes toolbox in MATLAB [64]. The fit assumed guess and lapse rates of 0.01%. The point of subjective equality (PSE) was defined as the stimulus rate of growth from the fit corresponding to the 0.5 response probability. 95% confidence interval error bars of the PSE were computed via a parametric bootstrapping procedure: the fitted psychometric function was resampled 400 times to generate a distribution of parameter estimates, and we determined the 2.5th and 97.5th percentiles of the simulated parameter estimates.

Eye Motion Data Analysis.

We computed the pursuit gain, defined as the subject’s pursuit velocity divided by the target’s velocity. The velocity was determined by computing the linear regression coefficient for the horizontal eye or stimulus positions over time. In trials with saccades, we determined the regression coefficients during the pursuit epochs between saccades, only evaluating epochs that were 80 ms (40 frames) or greater. A gain of one means that the target was correctly locked onto the fovea for the duration of the trial. Gains less than one indicate that the subject’s eye velocity was slower than the target, and gains greater than one indicate that the subject’s eye velocity was faster than the target. Note that “gain” in this context differs from “Gain” used in Chapters 1-3; we distinguish the two through capitalization.

4.3 Results

Fig. 4.2 shows psychometric fits from a single subject in the pursuit (Fig. 4.2, solid-magenta) and control (Fig. 4.2, dashed-teal) experiments. The y-axis is the response probability and the x-axis is the test stimulus rate-of-growth. In Fig. 4.2A, the leading bar was the test stimulus in the top panel; while the trailing bar was the test stimulus in the bottom

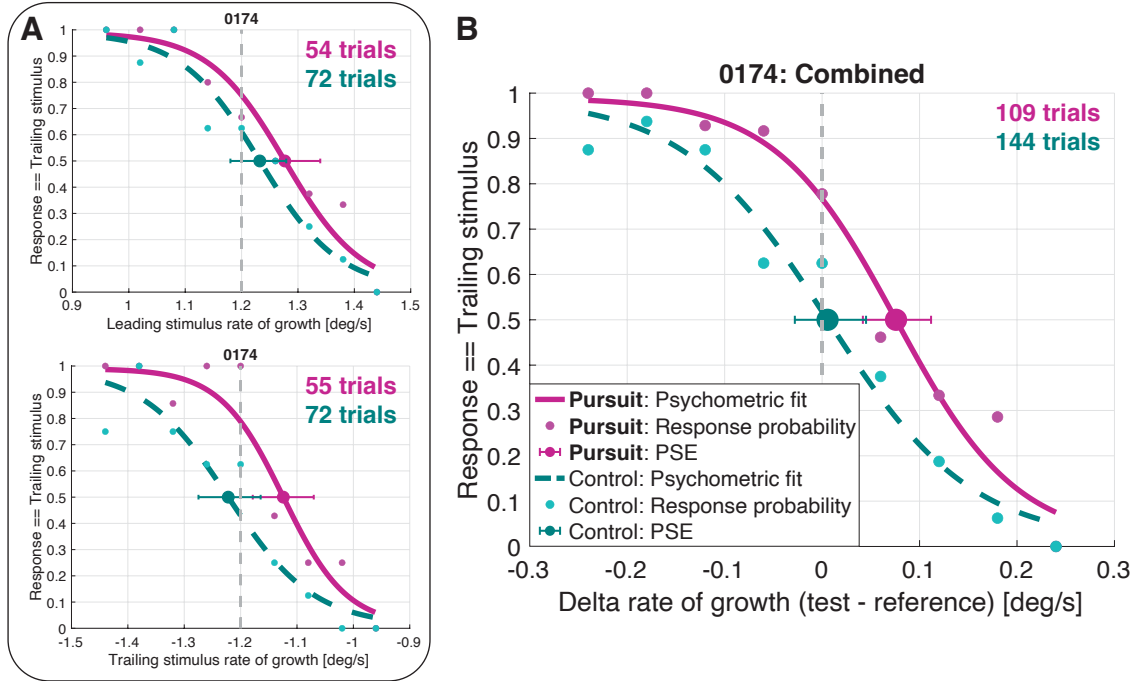


Figure 4.2: Example psychometric functions from one subject. The solid-magenta markers indicate results from the pursuit experiment and the dashed-teal markers indicate results from the control experiment. The y-axis is the response probability and the x-axis is the test stimulus rate-of-growth. The small symbols indicate the average response probabilities, and the large symbols indicate the point of subjective equality (PSE) with 95% confidence interval error bars. The vertical light-gray dashed-line indicates the reference rate of growth. (A) The leading bar was the test stimulus in the top panel; while the trailing bar was the test stimulus in the bottom panel. The sign of the x-axis indicates the direction of growth relative to the pursuit target: positive indicates growth in the same direction as the pursuit target and negative indicates growth in the opposite direction. (B) We additionally combined both graphs in A, by subtracting the reference growth rate (1.2 and -1.2 , respectively) from the x-axis values. In the combined graph, the x-axis is the delta rate of growth (test - reference). For subject 0174, the PSE in the control experiment was on average located at the point where the bars grew at equal rates in the world; while the PSE in the pursuit experiment was shifted right.

panel. The sign of the x-axis indicates the direction of growth relative to the pursuit target: positive indicates growth in the same direction as the pursuit target (relevant for the leading stimulus) and negative indicates growth in the opposite direction (relevant for the trailing stimulus). The small symbols indicate the average response probabilities, and the large symbols indicate the point of subjective equality (PSE) with 95% confidence interval error bars. The vertical light-gray dashed-line indicates the reference's rate of growth, the point at which the two bars grow at equal rates in the world. If the subject can correctly identify when the bars are growing at equal rates, then we would expect the PSE to lie along this line. We additionally combined both conditions by subtracting the reference growth rate (1.2 and -1.2 , respectively) from the x-axis values. In the combined graph, the x-axis is the delta rate of growth (test $-$ reference), shown in Fig. 4.2B. Results for all subjects are reported in Appendix 1, Figs. 4.5 and 4.6.

For subject 0174, the PSE in the control experiment (Control-PSE) was on average equal to the reference's rate of growth, the point where the bars grew at equal rates in the world (Fig. 4.2B, dashed-teal); while the PSE in the pursuit experiment (Pursuit-PSE) was shifted right (Fig. 4.2B, solid-magenta). This rightward shift suggests that: 1) the leading bar would have to grow faster in order to be perceived as growing at the same rate as the trailing bar; and 2) the trailing bar would need to grow slower in order to be perceived as growing at the same rate as the leading bar.

Nine of the ten other subjects showed a similar trend; however, for most of the subjects, the PSE's in both experiments were shifted left, with the Pursuit-PSE showing a less leftward shift (more rightward) than the Control-PSE, shown in Appendix 1, Figs. 4.5 and 4.6. This bias may be explained as follows: The pursuit target always moves $6^\circ/\text{s}$ and the leading and trailing bars grow outward from the target. For the leading and trailing bars to grow at the equal rates ($\pm 1.2^\circ/\text{s}$), the leading bar's right edge would move $7.2^\circ/\text{s}$ while the trailing bar's left edge would move $4.8^\circ/\text{s}$. Since the leading bar's edge speed is faster, subjects may have been biased to select the "faster moving edge" instead of the "faster growing bar". However, this bias would have been present in both the control and pursuit experiments, thus to account for the bias, we subtracted the [Pursuit-PSE $-$ Control-PSE].

Fig. 4.3 plots the [Pursuit-PSE $-$ Control-PSE] for all subjects. Each small symbol represents one subject and the large symbol represents the average with 95% confidence interval error bars. The horizontal light-gray dashed-line indicates the point where the Pursuit-PSE = Control-PSE, positive values indicate that the Pursuit-PSE was shifted further to the right than the Control-PSE, and negative values indicate that the Pursuit-PSE was shifted further towards the left. On average, the Pursuit-PSE was shifted towards the right ($p = 0.0086$, paired t-test) and additionally, the lower 95% confidence interval error bar was above 0. This suggests that under conditions in which the leading and trailing bars grew at equal rates in the world, the subjects perceived the trailing bar as growing faster by about 4% (Fig. 4.3). Thus, this suggests that the trailing bar, by growing in a direction consistent with retinal slip, gave rise to the "illusion of relative stability".

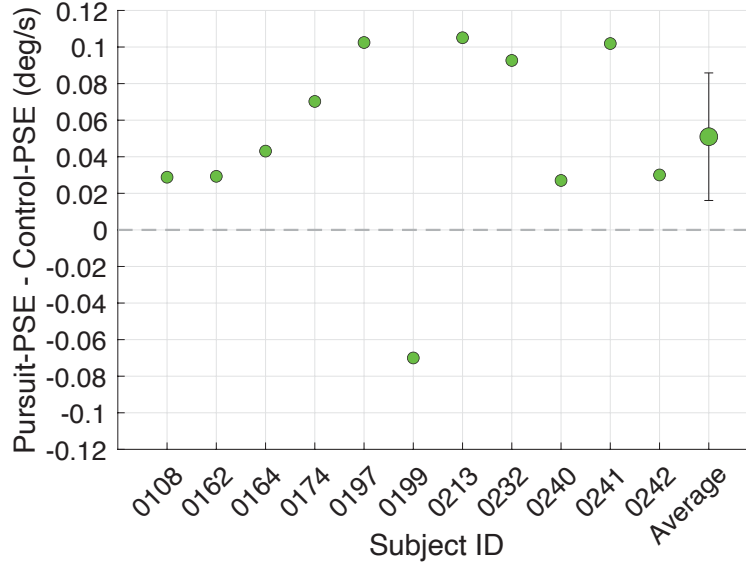


Figure 4.3: Subtracting [Pursuit-PSE – Control-PSE] for 11 subjects. Each small symbol represents one subject and the large symbol represents the average with 95% confidence interval error bars. The horizontal light-gray dashed-line indicates the point where the Pursuit-PSE = Control-PSE. On average, the Pursuit-PSE was shifted towards the right ($p = 0.0086$, paired t-test), suggesting that under conditions in which the leading and trailing bars grew at equal rates in the world, the subjects perceived the trailing bar as growing faster.

Additional Analyses: Evaluating Eye Motion.

Pursuit Gain Analysis.

We verified that the subjects’ performed the correct eye motions by computing the pursuit gains. For the pursuit experiment, a gain close to one was especially important since maintaining proper pursuit gave rise to the retinal motions that we aimed to establish. Specifically, for gains ≤ 0.8 , the trailing bar would no longer move in a direction consistent with retinal slip and therefore no longer addresses the research question. In contrast, for the control experiment, a gain ≤ 0.8 was important because we were specifically aiming to measure perceived motion without pursuit, to disrupt the retinal directions of the stimuli.

For each experiment, we fit a Gaussian to the histogram distribution of gains across all trials for each subject, determining the average and standard deviation. Fig. 4.4A plots the pursuit gain for each subject, each symbol is the average of the Gaussian with SD error bars. The solid-magenta symbols indicate results from the pursuit experiment and the hollow-teal symbols indicate results from the control experiment. Pursuit gains of 1 and 0.8 are indicated by the horizontal light-gray solid- and dashed-lines, respectively. On average, the pursuit gains were greater than 0.8 for the pursuit experiment (Fig. 4.4A, solid-magenta) and were

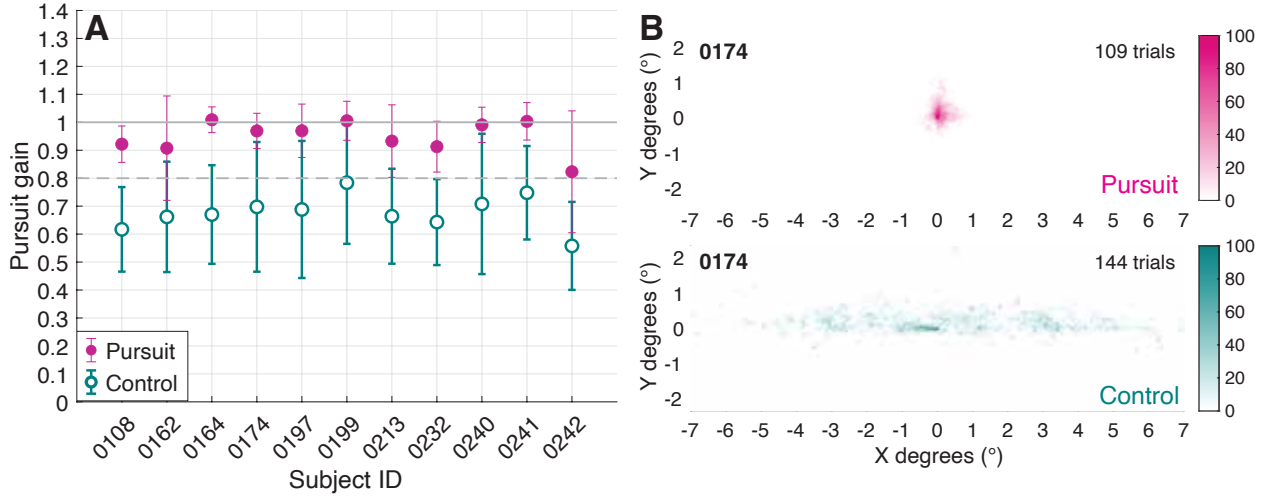


Figure 4.4: Eye motion analyses. (A) Pursuit gains for 11 subjects. Each small symbol represents the average gain with SD error bars, which were determined by a Gaussian fit to the distribution of gains for each experiment. The solid-magenta symbols indicate results from the pursuit experiment and the hollow-teal symbols indicate results from the control experiment. Pursuit gains of 1 and 0.8 are indicated by the horizontal light-gray solid- and dashed-lines, respectively. On average, the pursuit gains were greater than 0.8 for the pursuit experiment and less than 0.8 for the control experiment. (B) Example eye position heat maps for one subject during pursuit (magenta) and control (teal) experiments. The data were combined across leftward and rightward pursuit directions and are plotted as if pursuit were rightward. The origin (0,0) represents the position of the pursuit target for the pursuit experiment or the white gap between the black bars for the control experiment. Positive x-values indicate positions to the right and negative x-values indicate positions to the left. Warmer colors indicate regions viewed more frequently.

less than 0.8 for the control experiment (Fig. 4.4A, hollow-teal). We note that subject 0199's control experiment gain was close to 0.8, which may have contributed in part to the results in Fig. 4.3. Subject 0242's pursuit experiment gain was close to 0.8 which could have been due to the high number of saccades, 96% of the trials contained saccades: we dropped 47% due to large (greater than 1°) and backward saccades, of the remaining trials only 6 were pure pursuit.

To better visualize the gains, we additionally plotted eye position heat maps. This was achieved by subtracting the slope of the pursuit target traces ($\pm 6^\circ/\text{s}$), binning the eye positions into a 2D grid, computing how often the eye position fell into each bin, and converting the counts into a percentage. Fig. 4.4B shows examples for one subject during the pursuit (magenta) and control (teal) experiments. The data were combined across leftward and rightward pursuit directions and are plotted as if pursuit were rightward. The origin (0,0) represents the position of the pursuit target for the pursuit experiment or the white

gap between the black bars for the control experiment. Positive x-values indicate positions to the right and negative x-values indicate positions to the left. Warmer colors indicate regions viewed more frequently. The heat maps for all subjects can be found in Fig. 4.8 in Appendix 1.

Evaluating the Saccade Filtering Criteria.

In addition, we evaluated the impact of the saccade filtering criteria on the results. Fig. 4.7 in Appendix 1, presents four analyses: (A) original results (no filtering); (B) results after filtering large (greater than 1°) horizontal saccades; (C) results after filtering large and backward horizontal saccades; and (D) results after filtering all saccades. Each small symbol indicates the [Pursuit-PSE – Control-PSE]. The number of trials included in the pursuit experiment is listed under each symbol. (As a reminder, saccade filtering was applied only to the pursuit experiment; all 144 trials were included in the control experiment.) The large symbol represents the average with 95% confidence interval error bars.

Filtering all saccades substantially reduced the number of trials, making the results less robust; for example, we excluded subject 0242 because only six trials remained after filtering. We report results in Fig. 4.7D, but caution interpretation.

The average Pursuit-PSE was shifted towards the right in the original results ($p = 0.041$, paired t-test) (Fig. 4.7A); more strongly in the results after filtering large saccades ($p = 0.012$, paired t-test) (Fig. 4.7B); and most strongly in results after filtering both large and backward saccades ($p = 0.0086$, paired t-test) (Fig. 4.7C).

The lower 95% confidence interval error bar is close to zero in the original results (Fig. 4.7A), and deviates above zero after filtering large saccades (Fig. 4.7B), and more so after filtering both large and backward saccades (Fig. 4.7C).

These results suggest that large (greater than 1°) and backward saccades disrupt the illusion, as the Pursuit-PSE shift was largest when these saccades were removed.

4.4 Discussion

Our findings help to explain those of Turano & Heidenreich (1996) [83] and demonstrate that the visual system suppresses the perceived motion of images moving in a direction consistent with retinal slip during smooth pursuit. To further understand the process, we first review several factors that influence motion perception during smooth pursuit eye movements.

Motion Perception and Misperception During Smooth Pursuit.

When a person is tracking a moving object, the visual system attempts to match the velocity of the eye to that of the moving object [72]. If successful, the retinal motion of the object would be zero, and the world-fixed background would sweep across the retina with a velocity equal to the eye motion. To recover the motion of the world and object, the visual system

could combine the retinal input with an eye movement signal to determine that the object is moving and that the world-fixed background is stable [84, 35]. Both estimated retinal motion and pursuit eye motion are considered noisy signals [29], and the magnitude of these errors can give rise to misperceptions of world (Filehne illusion) and object (Aubert-Fleischl phenomenon) motion during smooth pursuit.

Filehne Illusion and Aubert-Fleischl Phenomenon.

When a person is tracking a moving object, the background scene appears to move opposite to the eye movement, rather than appearing stationary, a phenomenon called the Filehne illusion [26]. A moving object appears slower during smooth pursuit than when the observer fixates and the same motion traverses the retina, an illusion called the Aubert-Fleischl phenomenon [7, 27]. In both of these illusions, perceived velocity is influenced by errors in the extra-retinal eye velocity signal [87] and the retinal motion signals; notably, both are affected by the stimulus' spatial frequency content [29].

Motion Perception Models of Pursuit.

Freeman & Banks [29] modeled these errors in the extra-retinal (e) and the retinal motion (r) signals to estimate the perceived world velocity of any given feature in a scene ($\hat{H}$) during smooth pursuit. $\hat{H}$ is equal to the linear combination of the retinal image velocity ($\mathbf{R}$) plus the eye velocity ($\mathbf{P}$), both modified by gains r and e , shown in Equation 4.1.

$$\hat{H} = r\mathbf{R} + e\mathbf{P} \quad (4.1)$$

Since $\mathbf{H} = \mathbf{R} + \mathbf{P}$, the estimated speed in the world, $\hat{H}$, is equal to the actual speed $\mathbf{H}$ adjusted by the gains r and e :

$$\hat{H} = r\mathbf{H} + \mathbf{P}(e - r) \quad (4.2)$$

We implemented these equations in the context of this study, assuming a rightward pursuit eye movement. Considering that the pursuit target moves $6^\circ/\text{s}$, the left edge of the trailing bar moves $4.8^\circ/\text{s}$ and the right edge of the leading bar moves $7.2^\circ/\text{s}$. These are the equations of these three edges:

- $\hat{H}_T$ is the estimated speed of the left edge of the trailing bar.
- $\hat{H}_P$ is the estimated speed of the pursuit target.
- $\hat{H}_L$ is the estimated speed of the right edge of the leading bar.

$$\begin{aligned} \hat{H}_T &= r(-1.2) + 6(e) \\ \hat{H}_P &= 6(e) \\ \hat{H}_L &= r(1.2) + 6(e) \end{aligned} \quad (4.3)$$

We subtracted $\hat{H}_P$ from both $\hat{H}_L$ and $\hat{H}_T$ to compute the perceived speed of $\hat{H}_T$ relative to $\hat{H}_L$:

$$\begin{aligned}\hat{H}_T - \hat{H}_P &= -1.2r \\ \hat{H}_L - \hat{H}_P &= 1.2r\end{aligned}\tag{4.4}$$

Equation 4.4 predicts that r would be the same for the motion of both the leading and trailing bars. Perceptually, our results showed that this was not the case. Instead, the results presented in this chapter suggest that the r for $\hat{H}_L - \hat{H}_P = 1.2r$ has to be smaller than the r for $\hat{H}_T - \hat{H}_P = -1.2r$. Future work could explore this further.

Comparison With Previous Work.

Souman et al. [80] used a matching task to quantify the perceived speed and direction of random dot patterns during smooth pursuit eye movements. They reported that there exists one compensation mechanism for both collinear and noncollinear stimulus motions, but the study did not explore the perceived motion of when two stimuli move collinearly with equal speeds with respect to eye motion, but in opposite directions.

Their conditions most relevant to our study measured motion perception when the random dots moved collinearly; moving horizontally (vertical speed $0^\circ/\text{s}$) at either $8^\circ/\text{s}$ (Fig.5: Exp 1, orange) or $12^\circ/\text{s}$ (Fig.8: Exp 2, orange). However, the pursuit speeds differed between these two conditions: $10^\circ/\text{s}$ in the former and $5^\circ/\text{s}$ in the latter. In the former case, the stimuli moved with Gain +0.7, slipping opposite to retinal motion by $-2^\circ/\text{s}$; and in the latter case the stimuli moved with Gain +2.4, moving in advance of eye motion at $7^\circ/\text{s}$. (Note that in this context, “Gain” refers to the magnitude of motion of the stimulus in the world, relative to the eye motion, in line with terminology used in Chapters 1-3.) For both cases, the perceived motion was underestimated by approximately 50%, which is unpredicted in the context of this chapter.

The studies in Chapters 2 and 3 along with previous work [5], found that images moving in a direction consistent with retinal slip appeared relatively stable, *regardless of amplitude*; the illusion persisted even for stimuli moving with 2.5x the retinal slip of a world-fixed image. During smooth pursuit, the illusion did not persist when images move with amplified retinal slip. Turano & Heidenreich (1996) [83] found that when the eye moved opposite to their grating stimulus (amplified retinal slip), the speed discrimination thresholds changed in a manner consistent with the transformed retinal speed due to pursuit eye movements. Souman et al. [80] quantified that subjects even overestimated the motion of images moving with amplified retinal slip, in line with the prediction of the Filehne illusion. This suggests that the “illusion of relative stability” exists during smooth pursuit, but not regardless of amplitude. Turano & Heidenreich (1996) [83] and this present study show that it only exists for images that move in the same direction as pursuit but with a slower speed (Gains between 0 and 1). This emphasizes the differences in the mechanisms underlying perception of motion and stability between fixational drift and smooth pursuit.

Effects of Saccades on Motion Perception.

For the pursuit experiment, we removed trials with large (greater than 1°) horizontal saccades. We additionally removed trials with backward saccades: Our hypothesis is that images moving in a direction consistent with retinal slip give rise to the “illusion of relative stability”, it was therefore crucial to remove trials with backward saccades as they may change the direction the images move with respect to eye motion. However, even with these filtering steps, the presence of trials with small forward saccades may have confounded the results as saccades are known to affect motion perception and spatial position judgments [45, 46, 47, 60]. We analyzed the results after removing all trials with saccades, results are shown in Fig. 4.7D. As mentioned in section **Evaluating the Saccade Filtering Criteria**, filtering all saccades substantially reduced the number of trials, making the results less robust, but for the subjects with sufficient trials (> 50), the trends are generally similar to those when we removed large and backward saccades (Fig. 4.7C and Fig. 4.3).

4.5 Conclusions

We showed that during smooth pursuit, the direction an object moves with respect to eye motion is an important parameter in giving rise to perceptions of motion. Images moving opposite to pursuit motion, in a direction consistent with retinal slip, were perceived as lagging more compared to images moving in advance of pursuit motion. This work extends insights from fixational drift research to pursuit eye movements, and adds to the list of factors that govern how motion is perceived during smooth pursuit.

4.6 Appendix 1

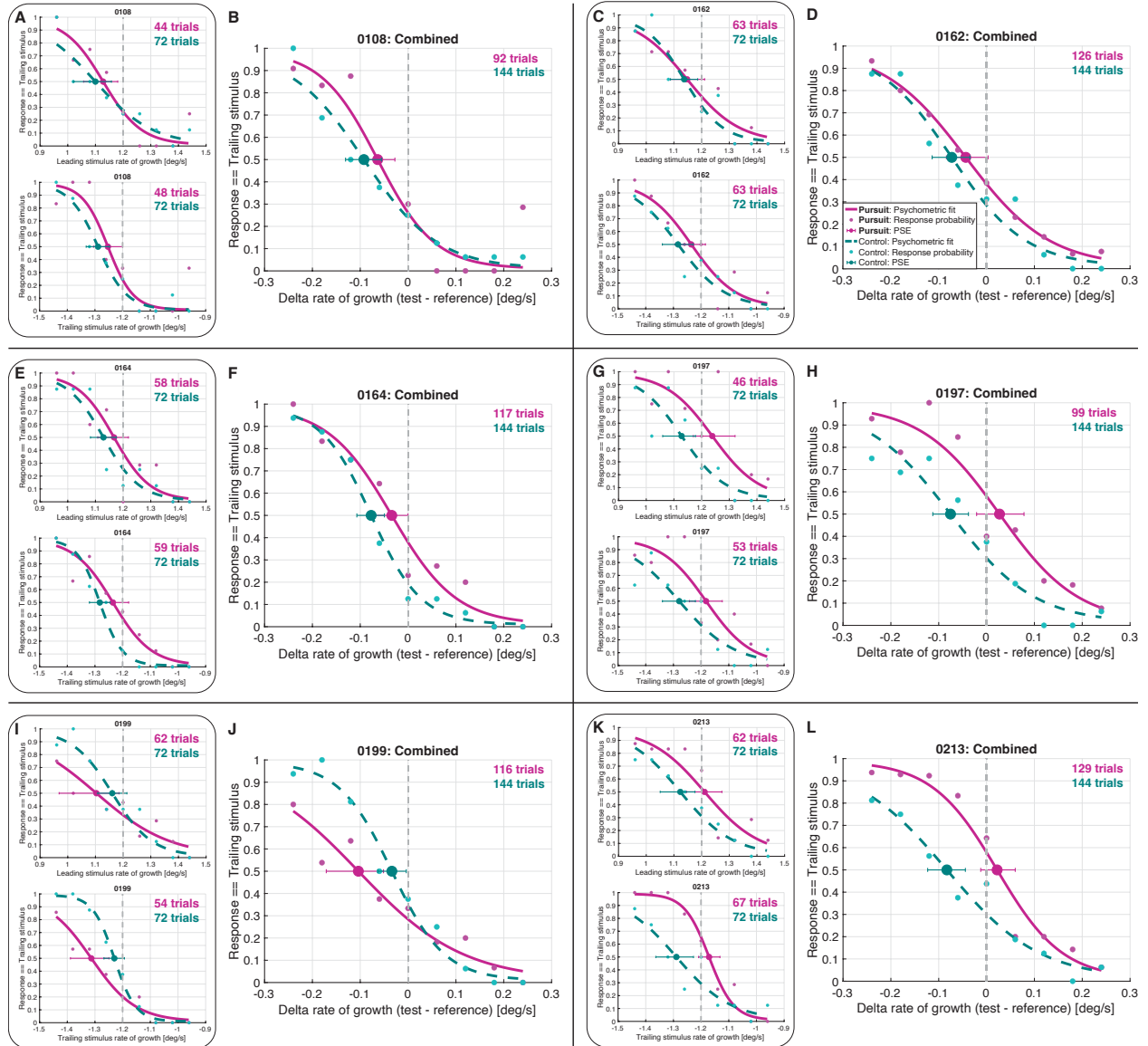


Figure 4.5: Psychometric functions from 6 subjects. The solid-magenta markers indicate results from the pursuit experiment and the dashed-teal markers indicate results from the control experiment. The y-axis is the response probability and the x-axis is the test stimulus rate-of-growth. The small points are the average response probabilities at each rate tested, and the large points are the point of subjective equality (PSE) with 95% confidence interval error bars. The vertical light-gray dashed-line indicates the reference rate of growth. In the combined graph, the x-axis is the delta rate of growth (test - reference).

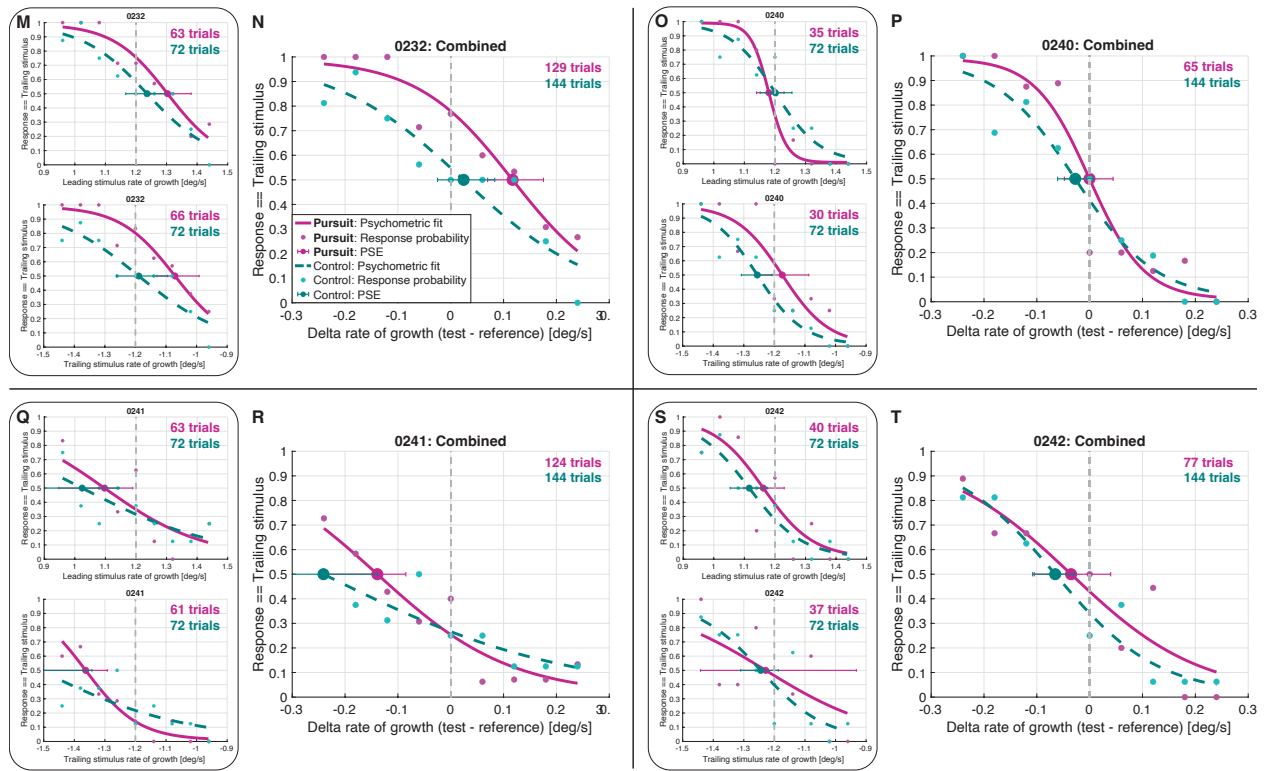


Figure 4.6: Psychometric functions from 4 subjects. (Fig. 4.5 continued).

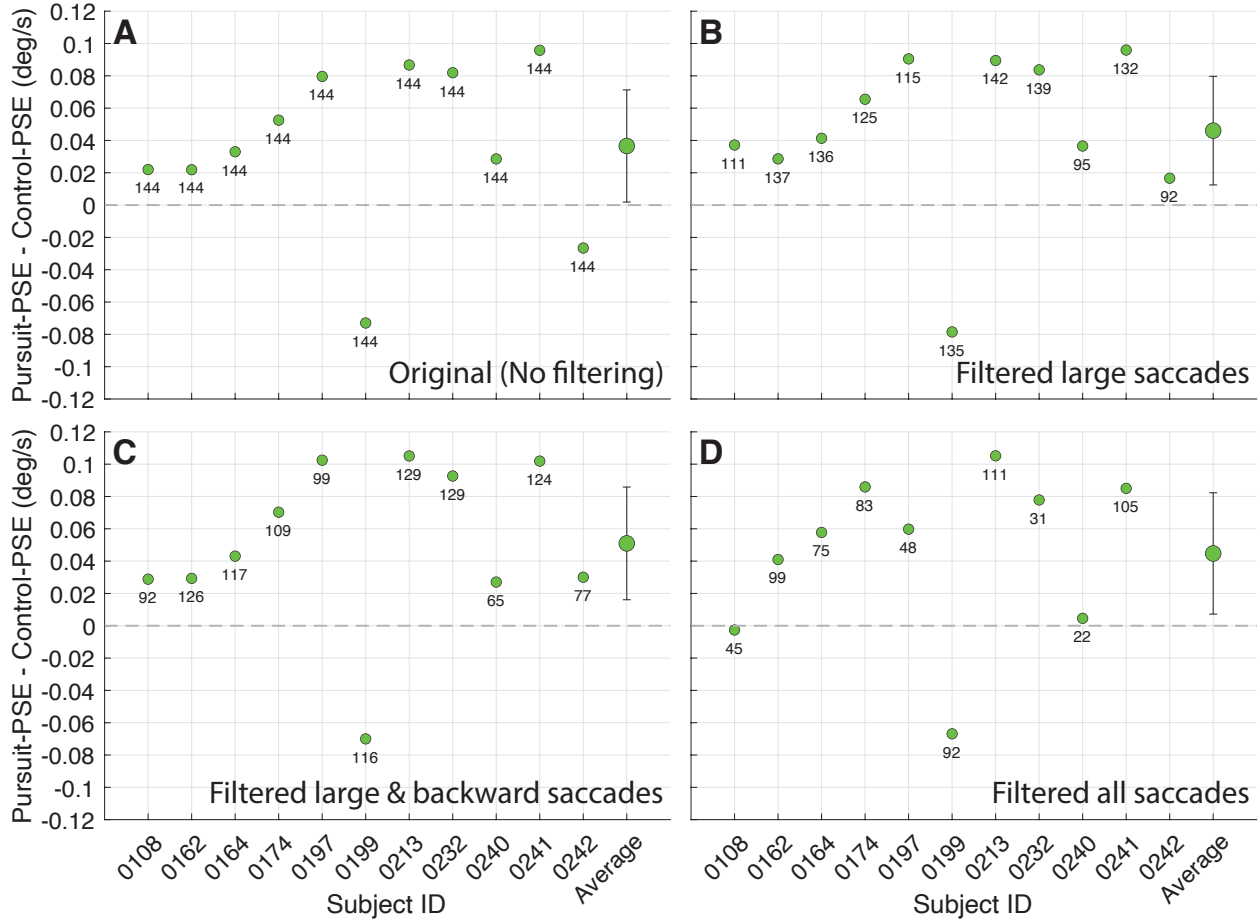


Figure 4.7: Evaluating the Saccade Filtering Criteria: (A) original results (no filtering); (B) results after filtering large (greater than 1°) horizontal saccades; (C) results after filtering large and backward horizontal saccades (also shown in Fig. 4.3); and (D) results after filtering all saccades. Each small point is the [Pursuit-PSE – Control-PSE]. The number of trials included in the pursuit experiment is listed under each point. (As a reminder, saccade filtering was applied only to the pursuit experiment; all 144 trials were included in the control experiment.) The large point represents the average with 95% confidence interval error bars.

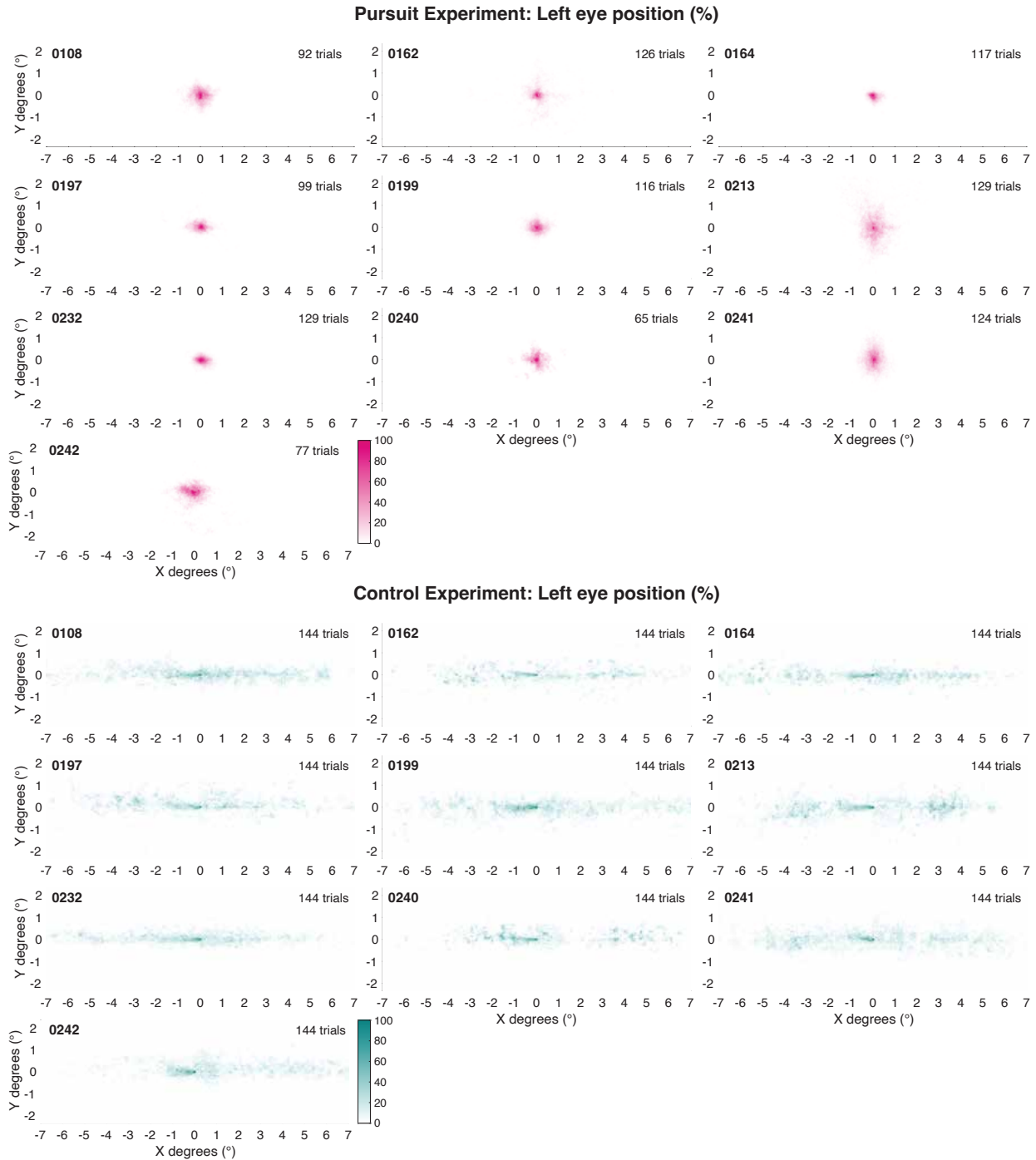


Figure 4.8: Eye position heat maps for 10 subjects during pursuit (magenta) and control (teal) experiments. The data were combined across leftward and rightward pursuit directions and are plotted as if pursuit were rightward. The origin (0,0) represents the position of the pursuit target for the pursuit experiment or the white gap between the black bars for the control experiment. Positive x-values indicate positions to the right and negative x-values indicate positions to the left. Warmer colors indicate regions viewed more frequently.

Acknowledgments

The authors thank Prof. Marty Banks for his helpful discussions. This research was supported by funding from National Institutes of Health Grants R01EY023591 (A.R.) and T32 EY007043 (J.C.D.), the Center for Innovation in Vision and Optics (civo.berkeley.edu) (J.C.D.), and a grant from the Minnie and Roseanna Turner Fund for Impaired Vision Research (J.C.D.).

Competing Interests.

None.

Author Contributions.

J.C.D., J.O.M., and A.R. designed research; performed research; and analyzed data. J.C.D. and A.R. wrote the paper.

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