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Retinal Image Motion and Visual Acuity

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Retinal Image Motion and Visual Acuity

by

Alisa Mae Nakashio Braun

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Professor William Tuten, Chair
Professor Jorge Otero-Millan
Professor Dennis Levi

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Abstract

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Fixational eye movements' (drift and tremor) utility has been long debated in the field of vision science. These small involuntary eye movements were traditionally thought to be artifacts of the visual system, but more recent research has revealed that adding a temporal aspect to vision through small changes in position over time may actually be beneficial in resolving fine detail. Using the adaptive optics scanning laser ophthalmoscope (AOSLO) to remove optical limits to acuity, we tested the most granular limits of human vision in various retinal motion conditions to help understand how drift and tremor reformat visual information at very fine spatial frequencies.

Chapter 1 provides an overview of the state of the literature in the field. This includes theories about why retinal motion is thought to be helpful to the perception of fine detail. Chapter 2 probes the time course over which these benefits accumulate. For movements to be useful, the eye and brain theoretically need to accrue changes in position over time. I show that this is indeed the case, and the utility of drift and tremor is dependent on stimulus duration. While retinal motion has been found to be beneficial, Chapter 3 introduces the notion that not all kinds of motion are useful to acuity. I show that this is also dependent on the characteristics of both the stimulus and retinal motion. Thus, eye movements can be detrimental to acuity if the stimulus features interact with eye movement magnitude and direction in a way that induces motion blur. In Chapter 4, I propose detailed methodology to probe the human contrast sensitivity function with and without eye movements to better understand the effect that eye movements have on visual perception. Chapter 5 provides a summary of this dissertation's work and broader impact on the field.

By utilizing advanced imaging techniques and carefully designed experiments, this work sheds light on the complex interplay between retinal motion and stimulus characteristics, ultimately contributing to a deeper understanding of the mechanisms underlying human vision.

To Kei Braun

My greatest achievement is the closeness we share. I love you!

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Acknowledgments

A PhD can mean many things. While most think of this milestone as an academic achievement, mine feels largely like a personal one. As I look back on my time in graduate school, the one thing that stayed consistent was the support of the many people in my life. Below is my attempt to thank each person who helped me on the path to this milestone.

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For this path forward, I am so grateful.

Chapter 1

General Introduction

1.1 Introduction to Fixational Eye Movements and Acuity

The eye is constantly in motion. Whether this is a bug or a feature of the visual system has been an area of intense debate for many years in the field of vision science. While some aspects of the role of human fixational eye movements (FEM) are beginning to be uncovered, the full impact of retinal image motion on visual acuity is not yet understood. There are numerous factors that contribute to the perception of high spatial frequency stimuli, including optics and sampling properties of the cone mosaic and downstream pathways. Fixational movements also add a temporal component to the encoding of spatial information by the visual system. While there are many examples of the body aiming to hold the visual world steady on the photoreceptor mosaic, there is also a clear benefit to dynamic vision. There are many known consequences of the introduction of a temporal aspect to seeing, as well as many areas left to study to better understand the implications of active vision.

The following chapters will examine how visual acuity changes with various stimulus parameters as a result of natural and artificial motion conditions. First, this dissertation will unpack the relationship between stimulus duration and visual resolution in natural compared to no retinal motion viewing conditions. We found that removing retinal motion only reduces performance on an acuity task when the stimulus was presented for an extended duration. This is a novel finding because it shows that removing retinal motion is not always detrimental to fine spatial vision. Thus, the benefits accrued from natural fixation are dependent on time, confirming predictions from computational studies. Next, the relationship between how a stimulus moves on the retina relative to its features will be discussed. We found that motion on the retina was not always helpful to acuity, as was apparent when the direction of motion was orthogonal to a stimulus's features. Performance was worst in this orthogonal motion condition, even compared to when double the amount of motion was applied. This introduces a new perspective to the current field, which for the most part assumes motion is beneficial to acuity. We show that this is dependent on a stimulus's features. Lastly, we

will outline a proposed method to investigate the full contrast sensitivity function for stimuli under natural and no retinal motion conditions.

1.2 Fixational Eye Movements

During fixation, the eye holds steady over an area of interest. These periods of fixation are interrupted by saccades, which move the eye ballistically across the visual field. Microsaccades have historically been thought to 'serve no useful purpose' (Kowler & Steinman, 1980). Today they are understood as a critical aspect to vision, especially useful in relocating gaze to areas of interest (Liversedge & Findlay, 2000). Microsaccades can be thought of as smaller saccades, fast eye movements that are made to change fixation position. While their relationship to saccades have been intensely disputed, they seem to share an underlying neural mechanism and serve a similar purpose (Martinez-Conde et al., 2013). When fixating while being asked to make a fine spatial judgment, the eyes microsaccade to and from points that are informative to task completion (Ko et al., 2010). They also aid in fine spatial vision by relocating the area with the most tightly packed photoreceptors – the fovea – over the stimulus being sampled (Poletti et al., 2013). Thus, the eye's saccadic movements are critical for fine spatial vision to counteract the negative consequences of a static retinal image. One example of the usefulness of FEM is that they prevent Troxler fading, a phenomenon in which a steadily-fixated object will begin to disappear from view in a matter of seconds. This is thought to occur because of adaptation to the unchanging retinal image; as soon as the subject makes a saccade, the perceived image intensifies (Martinez-Conde et al., 2013). Sensitivity is restored when fixational eye movements shift image features to new, unadapted photoreceptors. This same concept can be applied to other sensory systems, such as with tactile stimuli in Braille readers (Breidegard et al., 2008).

The eye's fixational movements between saccadic events are referred to as intersaccadic movements. This includes drift and tremor, the impact of which on visual acuity are still relatively not well understood. Drift movements are 0-40 Hz in frequency, usually vary between 4-50 arcmin/second and are around 1-4 minutes of arc in amplitude (Ditchburn, 1973; Nachmias, 1961; Rolfs, 2009). Tremor movements are quick 40-100 Hz oscillations, and have an amplitude of about 1 arcmin (Rucci & Poletti, 2015). Given the historic contentiousness of fixational saccades, the full purpose, mechanisms and perceptual implications for drift and tremor are understandably an area of intense debate.

1.3 Individual Differences in Fixational Eye Movements

Fixational motion can vary greatly between individuals, especially comparing naïve participants to those who are 'experts' and have had much practice fixating (Figure 1.1, Cherici et al., 2012). The difference ranges from a fixational span around 14 times smaller for

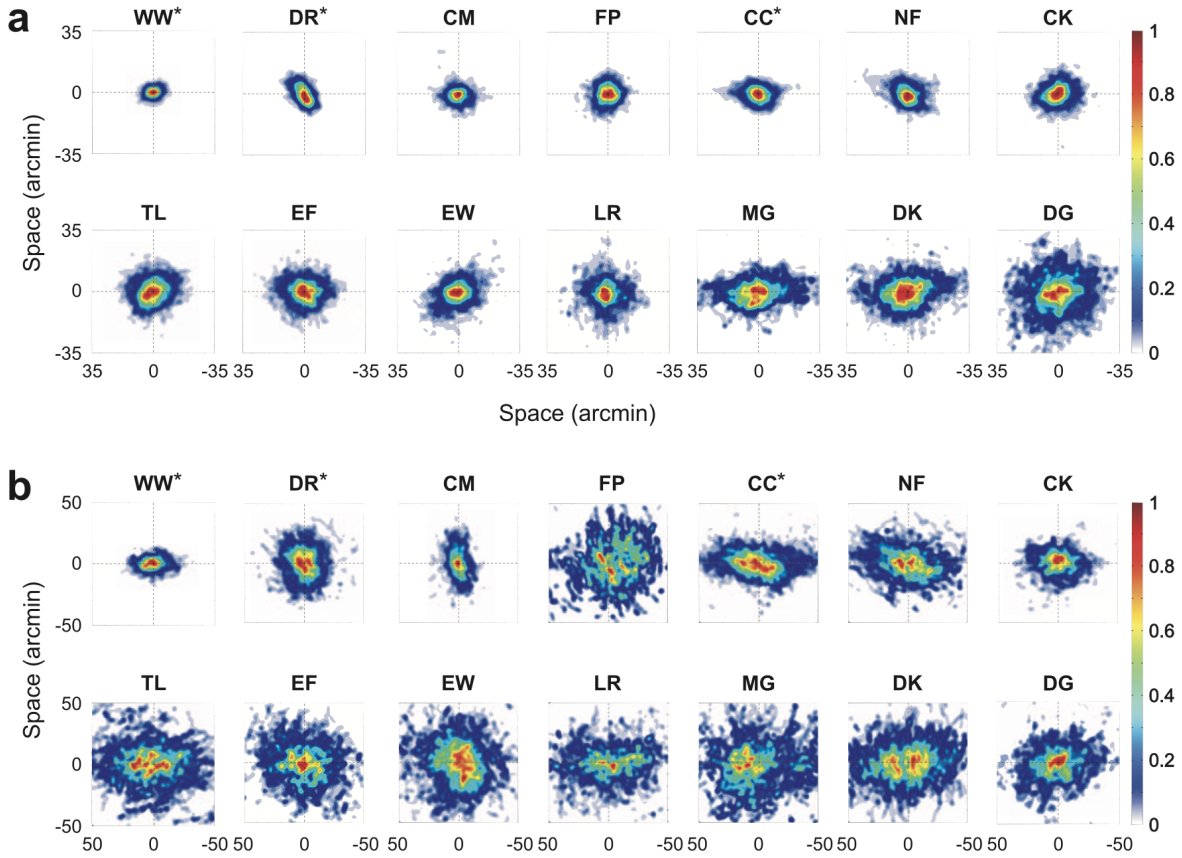


Figure 1.1: Individual probability density functions of eye movements during fixation (5 seconds). Panel A was a no marker condition, and panel B a fixation marker condition (Cherici et al., 2012).

trained compared to untrained subjects (Figure 1.1 b, subjects with asterisks mark the expert observers). This is especially important to note because most of this area research has historically relied on data from highly trained individuals. It is therefore likely that early studies generally underestimated the span of FEM (Rolfs, 2009). Individuals also have various anisotropies in their fixational patterns (1.1, a & b). Importantly, there are also large task dependent changes in FEM. When a fixation marker is present, saccades are less frequent, smaller in amplitude and drift is slower (Cherici et al., 2012). While intersubject differences are still seen while subjects view a fixation marker, overall fixational span is much smaller. The type of marker shown also changes the characteristics of fixation (Bowers et al., 2021a). Fixation also changes based on task demands; the amplitude of drift motion is longer and larger while performing active tasks (Bowers et al., 2021b). Microsaccades are also less frequent but larger with increased task difficulty (Siegenthaler et al., 2014). No matter the task or individual, there will always be motion in the eye that affects downstream processing of the visual world.

1.4 Optical and Neural Factors that Limit Acuity

The movement of the eye also interacts with several other early processes, including both optical and neural factors that influence fine spatial acuity. First, the retina's photoreceptor packing plays an important role in determining the highest spatial frequency that can be encoded by the cone mosaic. In order to resolve a fine stimulus, it is critical that its spatial frequency is not finer than the the neural units involved in sensing and processing such stimuli. If the receptor is not finely packed enough to discriminate features and send these signals to higher order visual processing areas, visual acuity will be bottlenecked at this first stage (Applegate, 2000). This limitation imposed by the packing of cells in the eye is referred to as the Nyquist sampling limit. In the fovea, cones dictate the limit of visual acuity. Briefly, this limit is derived from the underlying hypothesis that foveal cones establish one-to-one, "private-line" connections with downstream midget retinal ganglion cells (mRGCs). Thus, foveal vision is limited by the cone Nyquist limit. As eccentricity increases, multiple cones connect to one mRGC. This convergence thus imposes a limit to acuity that is introduced by post receptoral mechanisms. Thus, foveal vision is limited by cone spacing, while parafoveal resolution is dictated by mRGC spacing (Rossi & Roorda, 2010). Models of fine spatial vision account for eccentricity to factor in these bottlenecks that happen in early vision (Drasdo et al., 2007; Watson, 2014). Thus, visual acuity decreases with eccentricity, with small variations along all four meridians of the retina (Mackeben, 1999).

Importantly, theoretical calculations of the retinal limits to visual acuity assume a static, aberration-free image is projected onto the photoreceptor mosaic. Historically, this has been studied using interference fringes, which utilize a neon-helium laser that interacts to create light and dark patterns that are directly projected onto the back of the eye in order to bypass the inhomogeneities introduced by the lens and cornea (Campbell & Green, 1965; Charman & Simonet, 1997; Westheimer, 1960). These individually unique aberrations limit much of the visual system's ability to resolve small stimuli. First, higher order aberrations from inhomogeneities in the eye's optics introduced by the cornea and lens significantly distort high spatial frequency information. This limitation to acuity worsens with pupil size (Campbell & Green, 1965). The brain is adapted to an individual eye's unique inhomogeneities (Artal et al., 2004), and can even adapt to the introduction of blur (Webster et al., 2002). Still, the eye's imperfections significantly impair fine vision. Second, diffraction imposes limitations to discrimination of point source stimuli. This is dictated by both the wavelength of light entering the eye and pupil size. These two factors have been disentangled from one another by measuring the difference between perception of interference fringes and normally viewed stimuli (Campbell & Green, 1965). They can also be bypassed to achieve superhuman resolution by using adaptive optics (Liang et al., 1997; Poonja et al., 2005). Similarly, we have used an advanced optical system with built-in image correction technology to display an unaberrated (but still diffraction limited) stimulus on the back of the retina using an adaptive optics system. Thus, we can mitigate these factors critical for studying vision near the photoreceptor limit.

1.5 Motion on the Retina

One challenge to discriminating a moving visual world is that the visual system needs to differentiate between retinal image motion that is caused by movement in the world from that which is self-induced. While taking a walk, the visual system must differentiate between the whole scene moving from the body's forward displacement (optic flow), the vertical motion of the body as each step is taken, motion from the head as it moves side to side scanning a scene, the motion of stimuli moving within the scene (such as a car moving along a road) and motion from fixational eye movements. Critically, all of these factors combine to produce a single, dynamic pattern on the retina.

Multiple perceptual mechanisms must differentiate the source of the resulting retinal image motion. This process is separated into two parts – retinal and extraretinal motion sensing. There are two main theories that explain how extraretinal signals, which are used to derive the body's location in space, are thought to occur. The first is proprioception, a feedback signal. As the body moves in space, muscle proprioceptors send signals back to the brain. These signals are used to identify the body's position in the world (Wurtz, 2008). While gross body positioning can be derived from muscle contractions, proprioception seems to be less helpful with extremely small movements, such as in fixational eye motion (Murakami, 2006; Skavenski et al., 1979). A second extraretinal position cue is the efference copy of the eye's movement. This can be thought of as a copy of the outgoing muscle command used to inform the brain of where the eye will be. By knowing where the muscles will move the body, the brain can then build a map of where the body is in space. It seems that efference copy is an important component of deriving eye position (Sommer & Wurtz, 2008). Moreover, there is evidence that efference copy might be utilized by the visual system to calculate offsets of the retinal image over time (Zhao et al., 2023). However, the eye's fixational movements (including saccades) are generally considered to be too fine for the body to rely on extraretinal signals to gather accurate position information.

1.6 Biological Retinal Image Stabilization Methods

The head and body are constantly in motion - often in order to point our eyes towards a stimulus. There are many examples of external stimuli catching our attention, and the body and head turning so that we are able to leverage the visual system to capture what is otherwise not in clear view. While some types of motion can be beneficial, there are simultaneously many automatic efforts to minimize motion on the retina. These gaze stabilization movements include the optokinetic response and the vestibulo-ocular reflex. The optokinetic response is initiated by slippage on the retina. It utilizes the eye's smooth pursuit and saccadic movements to move the eye over a moving visual scene to keep an area of interest nearest to the center of the visual field. The vestibulo-ocular reflex relies on vestibular organs to move the eyes to counteract head and body movements. The result of these two reflexes is a stabilized gaze that makes the visual world clear even with head and body

motion (Carpenter, 1989). Thus, the body uses motion and stillness in parallel to optimally sample a scene.

1.7 History of Research Removing Retinal Motion

The first written account of image fading due to a lack of eye movements was reported in the early 19th century (Troxler & Himlyk Schmidt, 1804). While during the same century the idea of fatigue and afterimages was beginning to be discussed (Helmholtz, 1864), it was not until much later that the disappearance of objects in the absence of retinal image motion was more thoroughly experimentally tested (Riggs et al., 1953). Thus began the development of technology that stabilized an image on the back of the retina. During this time, optical lever based approaches dominated the field (Ditchburn & Ginsborg, 1952; Riggs et al., 1953). However, these approaches were often damaging to the eye itself because it required attaching a contact lens directly onto the eye's surface (Young & Sheena, 1975). Additionally, the physical presence of the lens and lever may have also disrupted natural fixational eye movements, limiting the amount the eye moved in experiments. Another early method of removing the effects of fixational eye movements was to induce (or study those with existing) ocular muscle paralysis (Brindley et al., 1975; Gilchrist et al., 1997). This is clearly very invasive and potentially harmful to research participants, especially for those who endured total body paralysis (Stevens et al., 1976).

Despite the risks to subjects, this early research was useful to establish that vision without retinal motion is deleterious to visual acuity and can even lead to a stimulus completely fading from view. Subsequent technological advancements allowed for better and less harmful eye tracking methods. The development of dual Purkinje image-based eye trackers was a large step for this area of research, as more natural movements could be accurately, safely and easily measured. These methods, paired with advancements in display technologies, have led to many studies utilizing low latency displays to account for FEM offsets while tracking the eyes motion in real time (Rucci & Desbordes, 2003). These studies remove the effects of motion over time by moving the stimulus with very little delay on a display while a subject is allowed to naturally view an image.

1.8 Effects of Removing Retinal Motion

There are perceptual effects beyond image fading and refreshing that are a result of the eye's smallest movements – drift and tremor (FEM will hereon only refer to drift and tremor). One line of work uses the adaptive optics scanning laser ophthalmoscope (AOSLO) to stabilize a stimulus on one patch of photoreceptors. This is achieved by moving the stimulus in the real world to compensate for any retinal displacement that might occur from natural fixational movements. When a high spatial frequency (60 CPD) stimulus is 'stabilized' so that the effects of drift and tremor are eliminated, performance decreases on an

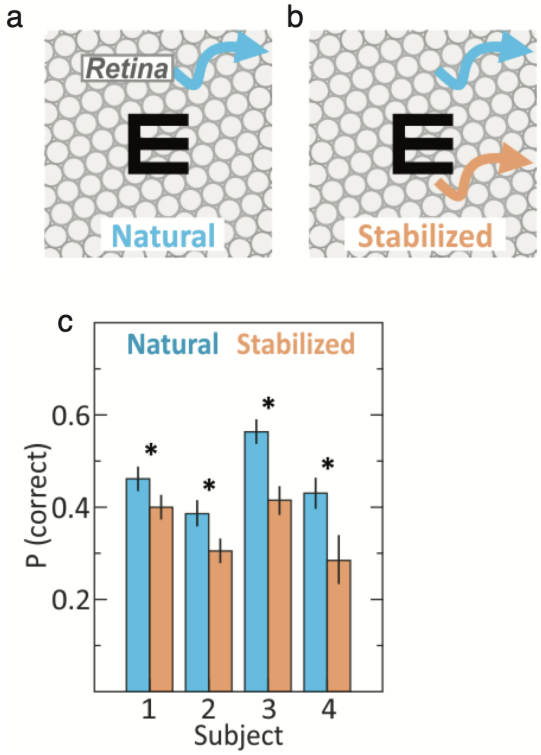


Figure 1.2: Performance was measured in natural (panel A) fixational eye movements or motion removed (stabilized, panel B) trials. Percent correct is shown between these two conditions in panel C (Ratnam et al., 2017).

acuity task when compared to natural viewing (Figure 1.2, Ratnam et al., 2017). Critically, this reduction was not due to decreased contrast, such as in longer-duration Troxler fading.

The effects of FEM also depend on the spatial frequency of the visual input. Human psychophysical work shows that the perception of medium (11 CPD) spatial frequency information is deleteriously affected by stabilization. This is not true of low (4 CPD) gratings, where stabilization has no effect on performance (Rucci et al., 2007). The direction of retinal motion is also an important factor to consider. Eye motion that is parallel to a stimulus's features are not helpful to visual perception. Specifically, one investigation presented tilted gratings to subjects while FEM-induced retinal image displacements were restricted in either a parallel or orthogonal axis to the grating's orientation. Percentage correct was higher when FEM orthogonal to the tilt of the stimulus were allowed. When the eye was only allowed to sample parallel stimulus features, the task became much more difficult, approaching the performance of fully stabilized stimuli (Rucci et al., 2007). We may see this effect because FEM reformat differences in contrast across time (Boi et al., 2017). When motion does not sample any changes in stimulus features, FEM are not useful. More broadly, when fine details in a stimulus are sampled by a moving retina, acuity improves.

1.9 Computational Approaches of Studying Dynamic Vision

The current literature posits two main benefits from natural fixational retinal image motion. First, computational work suggests that FEM help sample fine stimuli that are under-sampled by the photoreceptor mosaic (Anderson et al., 2020). Thus, if the eye is allowed to move naturally over time, photoreceptors can move over a stimulus which would otherwise be indiscriminable by individual rods and cones. Specifically, this model considers fine spatial frequency stimuli beyond the spatial resolution limit of the Nyquist limit. This is of particular interest to human psychophysical work studying the effects of FEM near the limit of spatial vision (Ratnam et al., 2017). Second, fixational movements serve to change inputs prior to any neural processing. They amplify high spatial frequency information inputs to the cortex, which help aid discrimination of these inputs (Boi et al., 2017). Drift and tremor also reduce redundancy in a natural scene, aiding the visual system in extracting meaningful features from the world (Kuang et al., 2012).

1.10 Adaptive Optics Scanning Laser Ophthalmoscopy: Stimulus Delivery

Adaptive optics scanning laser ophthalmoscopy is a useful tool for studying the effects of fixational eye movements for a number of reasons. First, integrated imaging and tracking in the AOSLO means otherwise unmatched precision in where the stimulus was projected. By visualizing each individual cone, exact certainty about photoreceptor-level sampling can be achieved. This means that stimulus delivery can be targeted to one patch of cones, and image-based analysis can confirm the accuracy of such retinal stimulation. Additionally, AO imaging techniques measure acuity under conditions where optical limitations to acuity are minimized. Thus, research can focus solely on receptoral and neural limits of vision.

1.11 Adaptive Optics Scanning Laser Ophthalmoscopy: Eye Tracking

Outputs from the AOSLO can be used to derive both extremely accurate and precise eye tracking. One method involves leveraging image registration algorithms to align sequentially acquired image information to a reference frame. This approach utilizes the scanning nature of the system to do stripe-wise correlations of the photoreceptor mosaic along the vertical axis (Stevenson et al., 2010). The system tracks eye motion within a few arcseconds of accuracy by registering each successive strip to a common reference frame (Stevenson & Roorda, 2005). The AOSLO can also characterize a stimulus's retinal trajectory by using image segmentation techniques to track the horizontal and vertical shifts of the negative

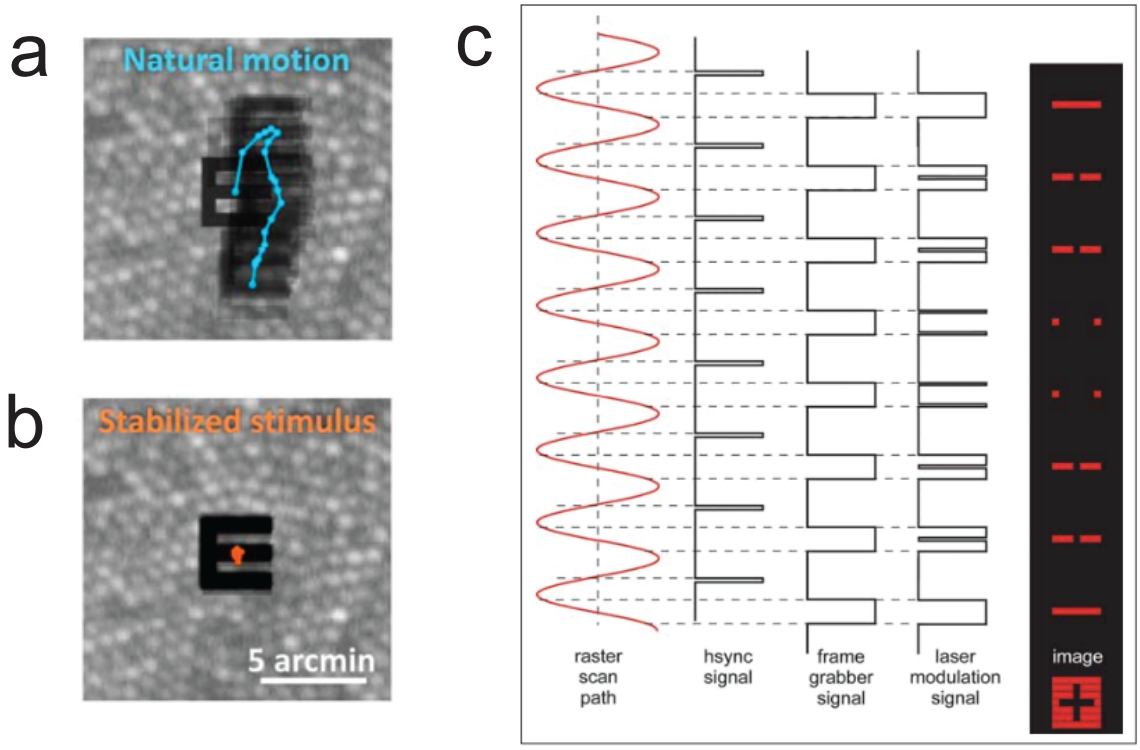


Figure 1.3: The top left panel (A) is an E that is fixed in the real world, with the trajectory that it follows with natural FEM plotted on the cone mosaic in blue. In the stabilized condition (panel B), the presentation of the stimulus is limited to a targeted cluster of cones in the AOSLO (Ratnam et al., 2017). Raster scanning and stimulus delivery techniques are shown in more detail in panel C. The subject is shown a red stimulus while the retinal image is simultaneously collected. The horizontal (15.4 kHz) and vertical (30 Hz) scanning simultaneously move the point source to create the stimulus on the back of the eye. The laser is then modulated to create a negative contrast image that is projected onto the back of the retina. The adaptive optics component of the system removes aberrations introduced by the cornea and lens, thus resulting in the projection of a diffraction limited stimulus (Poonja et al., 2005).

contrast optotype projected onto the retina across frames (Figure 1.3 a). By monitoring the movement of this optotype frame by frame, the system can deduce the stimulus motion at a 30 Hz sampling rate. Together, photoreceptor and stimulus-based tracking underscore the benefit of using the AOSLO to study the interplay between retinal image motion, neural sampling, and visual perception.

1.12 Adaptive Optics Scanning Laser Ophthalmoscopy: Retina-Contingent Stimulus Delivery

Using the AOSLO, the effects of fixational eye movements (Figure 1.3a) can be nearly eliminated by what is called 'stabilizing' a stimulus on the retina. Drift and tremor can be canceled out (Figure 1.3b) because the AOSLO places the stimulus at specific locations on the retina. Thus, the stimulus moves in the real world, but stays on the same patch of photoreceptors. This stabilizing motion is also referred to as gain 1 because the motion of the stimulus in the world precisely matches the motion of the eye, effectively canceling out any retinal motion. This can then be compared to the gain of 0 or 'natural' retinal motion condition, where the visual system samples a dynamic retinal image normally. The AOSLO is also able to move a stimulus in a predetermined amplitude and direction. Critically, this can be done in addition to the motion needed to stabilize a stimulus. We can then achieve an 'imposed motion' condition: normal FEM are removed with stimulus motion, and an arbitrary predefined motion is added in a particular direction. Thus, this image-based method uses modern tracking techniques at accuracies previously unachievable to test the effects of fixational eye movements.

1.13 Chapter 2: FEM and Stimulus Duration

As previously discussed, the eye's dynamic sampling of stimuli aid in fine spatial acuity. The length of the temporal window in which this information is gathered is critical to the usefulness of FEM. If the eye is only allowed to sample a stimulus for a short time, there should be little to no difference between viewing a static image and a dynamic one. Thus, there must be an inflection point in stimulus duration where drift and tremor become more useful to visual acuity.

Previous work has shown that when retinal motion is removed at long (750 and 1000 ms) stimulus durations, performance degrades (Ratnam et al., 2017; Rucci et al., 2007). If FEM help achieve better acuity, we would expect performance in stabilized viewing to degrade over time at longer durations. At short durations, we do not expect to see the benefits of eye movements to be present because the eye hasn't had time to make them. In the same vein, we should not see detriments when removing them. Short stimulus presentations were tested in 1976, but were found to not impact performance (Tulunay-Keesey & Jones, 1976). However, this study relied on dated (and invasive) contact lens mirror based stabilization methods. Cataloging the time course necessary to accrue the benefits of the moving retina motivated Chapter 2 of this dissertation.

1.14 Chapter 3: FEM Magnitude

While some retinal motion is useful for longer durations, it seems evident that not all motion should be helpful for visual acuity. At one end of the spectrum, it is abundantly clear that removing drift and tremor is deleterious to seeing fine stimuli (Ratnam et al., 2017; Rucci et al., 2007). However, an upper limit must also exist to beneficial drift and tremor, as too much motion (relative to stimulus spatial frequency) can induce motion blur (Demer & Amjadi, 1993; Packer & Williams, 1992). In short, one aspect of this area research that is still unclear is just how much retinal motion is beneficial for visual acuity. One study found that individuals who had less drift and tremor had better visual acuity (Clark et al., 2022). While this seems to suggest that more FEM are harmful to seeing fine details, there is of course the other side of the coin – stabilization impairs vision.

In natural fixation, the amount of motion used to sample a stimulus depends entirely on how much the eye moves. Therefore, in order to study how much motion is beneficial to the visual system, individual differences in natural motion must be removed. This motivated Chapter 3, where we removed all natural motion by stabilizing a stimulus on the retina and adding various amounts of stimulus motion to achieve precise control over stimulus retinal trajectory independent of how the eye is moving. Using these predetermined trajectories, we can then measure how much motion strikes the balance between helpful and harmful.

1.15 Chapter 4: FEM and the Contrast Sensitivity Function

The benefits of FEM are thought to depend on contrast. However, the contrast sensitivity function (CSF) has yet to be fully psychophysically cataloged with and without FEM using modern image-stabilization techniques. In addition, most research using the AOSLO to measure the effects of FEM on visual acuity has relied on using a tumbling E optotype. By removing the interactions between a horizontal and vertical component (such as exists in an E optotype), this effect of too much retinal motion blurring images should become even more apparent. Chapter 4 will lay the groundwork for future work to further extend the understanding of how FEM change the ability to resolve various contrasts.

Chapter 2

Stimulus Duration and Acuity at the Resolution Limit of the Parafoveal Retina

2.1 Introduction

The eye is constantly in motion, even during periods of careful fixation. As a result, the retinal image is never stable, moving incessantly across the mosaic of photoreceptors that capture light and generate the neural signals that give rise to vision. The impact of this retinal image motion on visual perception has been debated by vision researchers for more than a century, and is currently not fully understood. Early work suggested that these movements would "detract from the accuracy" of percepts (Hartridge, 1922), while others argued they were essential for acuity (Andersen & Weymouth, 1923; Averill & Weymouth, 1925).

One way to study the effects of these movements is to remove them experimentally. Efforts to stabilize (or remove retinal motion during natural viewing) an image on the back of the retina date back to the mid-1900s (Keesey, 1960), where short presentation times were found to not be impacted by stabilization (Tulunay-Keesey & Jones, 1976). Other investigations suggest that these small movements may actually negatively impact acuity by incurring blur (Packer & Williams, 1992).

Although most of the field at that time discounted fixational motion's effects as having 'no useful purpose' to vision (Kowler & Steinman, 1980), the past 20 years have seen a resurgence in work that seeks to better understand the full implications of the unsteady eye (Kuang et al., 2012; Rucci & Desbordes, 2003; Rucci & Victor, 2015). Our aim is to shed light on this long-standing question using the latest technology to remove the effects of fixational motion on the retina.

One vein of computational work suggests that as FEM move the eye, the visual system uses a Bayesian approach to inference that leads to improved visual acuity at longer durations

(Anderson et al., 2020). This same logic is leveraged in super resolution cameras to derive less noisy, sharper images (Farsiu et al., 2004). Supporting this work are studies that show that when the effects of retinal motion are removed, performance on acuity tasks is impaired (Ratnam et al., 2017; Rucci et al., 2007). Importantly, the dynamic sampling of photoreceptors may help encode information that might otherwise be lost as the visual world is sampled by discrete sampling units. Acuity is limited by local photoreceptor density near the foveal center, while farther out in eccentricity resolution is governed by the mRGC Nyquist limit (Rossi & Roorda, 2010). Thus, to achieve full perception of fine spatial features, the visual system should sample the world dynamically. This has led to an emergence of other theories on the usefulness of FEM. Recent work has shown that drift and tremor movements reformat the 1/f spatial frequency curve found in natural images at the retinal encoding stage (Field, 1987) enhancing the representation of high spatial frequency information. This 'whitening' (Rucci & Victor, 2015) is predicted to have beneficial effects on fine spatial vision. However, the effects of duration on the benefits of FEM are not well understood.

Theoretically, the visual system should need time to benefit from the movements of the unsteady eye. While this has been tested using computational approaches (Anderson et al., 2020), the field so far lacks human psychophysical data to prove these theoretical findings. Using an AOSLO to image the cone mosaic, track retinal motion, and present gaze-contingent stimuli with cellular precision, we tested various stimulus durations previously unexamined for retinal stabilization's effects on acuity. We also aimed to better understand trends in eye movement patterns that might lead to differences in performance at these short durations.

2.2 Methods

Participants

Subjects with no known retinal disease were included in two slightly different experimental data collection protocols. This included 4 subjects (three male, one female; ages 25-38) in a blocked data collection condition (Figure 2.1, top panel), and 3 subjects (two male, one female; ages 38-57, 1 subject from the first protocol) in an interleaved condition (Figure 2.2, bottom left panel). Informed consent was granted from each subject and all procedures adhered to the Declaration of Helsinki.

Apparatus & Stimuli

An adaptive optics scanning laser ophthalmoscope was used to present gaze-contingent stimuli to targeted areas of the photoreceptor mosaic and gather single-cone resolved image data from the retina (Roorda et al., 2002; Wang et al., 2019). All subjects were dilated with a 1% Tropicamide solution 15 minutes prior to the experiment. Subjects sat in the AOSLO system with their heads immobilized using a custom molded bite bar. Infrared light for imaging (wavelength: 840 $\pm$ 25 nm; luminance: $\sim$4 cd/m^2) and wavefront sensing (wavelength: 940 nm) was filtered from a supercontinuum laser source (SuperK Extreme; NKT Photon-

ics, Birkerød, Denmark). The visible 840 nm imaging laser was raster scanned horizontally at 16 kHz and vertically at 30 Hz, ultimately making the light visible to the subject as a dim red square. A Shack-Hartmann wavefront sensor and a 97-actuator deformable mirror (DM97-08; ALPAO, Montbonnot-Saint-Martin, France) were used to measure and correct for higher order aberrations, respectively. Image light reflected from the retina was collected by a photomultiplier tube (PMT) positioned behind a confocal pinhole. PMT signals were digitized at 20 MHz to produce a 512 × 512 pixel 30 Hz retinal image. The square imaging raster subtended 0.9 degrees, corresponding to 0.105 arcmin per pixel.

For each stimulus presentation, the laser was modulated at different intervals to produce a negative contrast 4-AFC tumbling E optotype. Each stimulus was displayed by modulation of the laser during the line scan of each frame. Thus, an E was rendered on the back of the retina during the 30 Hz frame for a portion of the full scan of the frame displayed to subjects (see 2.1, bottom panel). We use frames to more accurately describe the duration of each stimulus presentation, as well as durations to help compare to previous investigations (Ratnam et al., 2017) to our results.

Using the AOSLO, exact retinal sampling can be derived from output images, since modulating the imaging laser off to render the stimulus is encoded by the PMT as a low intensity at the corresponding pixels. Figure 2.1 depicts the photoreceptor mosaic where cones hexagonally tile the retina at 1 degree temporally with a negative contrast E. The nature of the stimulus delivery ensures that the stimulus is shown on this exact location on the retina. Subjects were instructed to report the orientation of the gaps of the optotype using a gamepad. Importantly, we can also track the motion of the retina in real-time using custom built software to nearly eliminate the effects of fixational eye movements (Yang et al., 2010). This is achieved by targeting stimulus presentation to the same patch of photoreceptors as the eye is allowed to naturally move. Trials in which the stimuli's position is moved in the world in order to stay on the same patch of cones throughout a trial are called 'stabilized' or have a gain of 1 in relationship to the eye's natural movement. Those that stay in world fixed coordinates are 'unstabilized' or gain 0.

Experimental Procedure

We used an orientation discrimination task to examine the effect of retinal stabilization on spatial vision. Similar to previous studies (Ratnam et al., 2017; Rucci et al., 2007), we opted to assess visual performance using a stimulus whose spatial properties remained fixed rather than adjusting its size to measure an acuity threshold.

First, all subjects sat for a 50-trial staircase guided by the Quest algorithm (Watson & Pelli, 1983) to determine the letter size that yielded 80% correct performance. Next, each subject completed 100 unstabilized and 200 stabilized trials using their unique threshold size for pseudorandomized blocks of 30, 60, 100, 375, 563 and 750 millisecond (1, 2, 3, 7, 11, 17 and 23 frame) stimulus durations (Figure 2.1, top). Subjects sat in for 100 trial blocks over multiple days with ample break time within and between blocks until tear film degradation began to have a negative effect on image quality or they self-reported fatigue. Additionally,

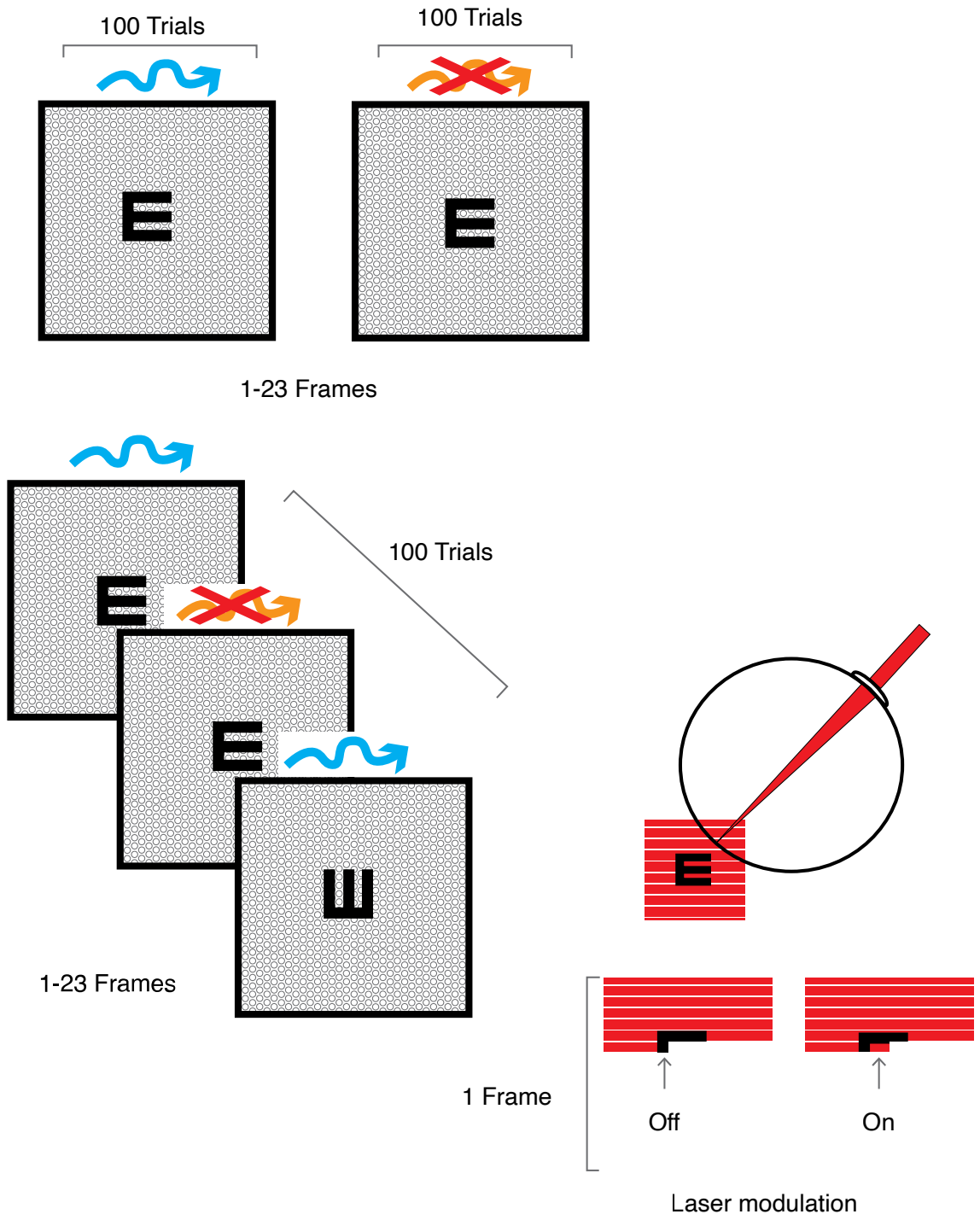


Figure 2.1: A tumbling E optotype was shown either in a blocked (top) or interleaved (bottom) design within a 100 trial block. These were either viewed as unstabilized or stabilized on the retina for 1-23 frames. The stimulus was shown in the AOSLO while the back of the retina was imaged via a line scanning raster. Subjects perceived a red field (.9 degrees) with a negative contrast E optotype made by modulating the laser as it scanned the retina (bottom right). Note that scanning continues until the full raster pattern is displayed.

we collected data in an interleaved protocol to mitigate the effects of localized cone fatigue – after a 50 trial staircase, 50 stabilized and 50 unstabilized trials were randomly shown through blocks of quasi-randomly shown durations at 30, 60, 100 and 750 ms (Figure 2.1, bottom). A mixed effects model indicated no statistically significant variation in performance between the two experimental designs ($p = 0.469$). The lack of significance suggests that the interleaved and blocked designs did not substantially impact overall performance, allowing us to merge datasets for a more robust and representative analysis.

Eye Movement Analysis

Eye motion was measured using custom made software which captures <1 min of arc motion traces at 30 Hz. Modulation of the imaging light creates a negative contrast stimulus on the retina, therefore ensuring a high-fidelity measurement of the stimuli's location on the photoreceptor mosaic. In stabilized trials, the eye's position at the time of stimulus delivery was derived from the location of the stimulus in world-fixed coordinates.

Trials were removed based on several criteria. First, images were filtered using custom software correlating a generated tumbling E stimulus to the image that was captured to account for distortions in the stimulus presentation from the AOSLO. Next, all stabilized trials were filtered to ensure that the stimulus was delivered as expected. First, we filtered the output image for our target stimulus at each trial's unique orientation. Using k-means clustering, the output image correlation was required to match the template ($r = .9$) of the tumbling E in 90% of the frames shown, or the trial was excluded. Next, data from stimulus durations longer than 2 frames were filtered for if the stimulus moved frame-by-frame either in real world or retinal coordinates by ± 1 standard deviation of the entire video's frame by frame motion. Unstabilized trials were only excluded if microsaccades or blinks occurred during stimulus presentation (Clark et al., 2022; Ratnam et al., 2017). The videos were then reviewed and excluded by hand to ensure accuracy.

2.3 Results

Results from the staircases (80% threshold) during natural viewing across subjects at various durations are shown in Figure 2.2. We show a decrease in letter size (MAR) as duration increases in unstabilized trials. This finding mirrors previous work, where MAR decreases with stimulus duration (Baron & Westheimer, 1973).

Each of these unique letter sizes (for each duration and subject) were then used to compare performance on different motion and duration conditions. Following previous investigations (Ratnam et al., 2017), we compared natural motion to stabilized viewing performance. The mean across subjects for each duration on unstabilized trials varied from 63-87%, with an overall mean performance of 75%, close to our intended target of 80%.

To account for the variability in subjects and durations, Figure 2.3 shows a ratio (stabilized/unstabilized) in performance between gain conditions by subject and duration. Mir-

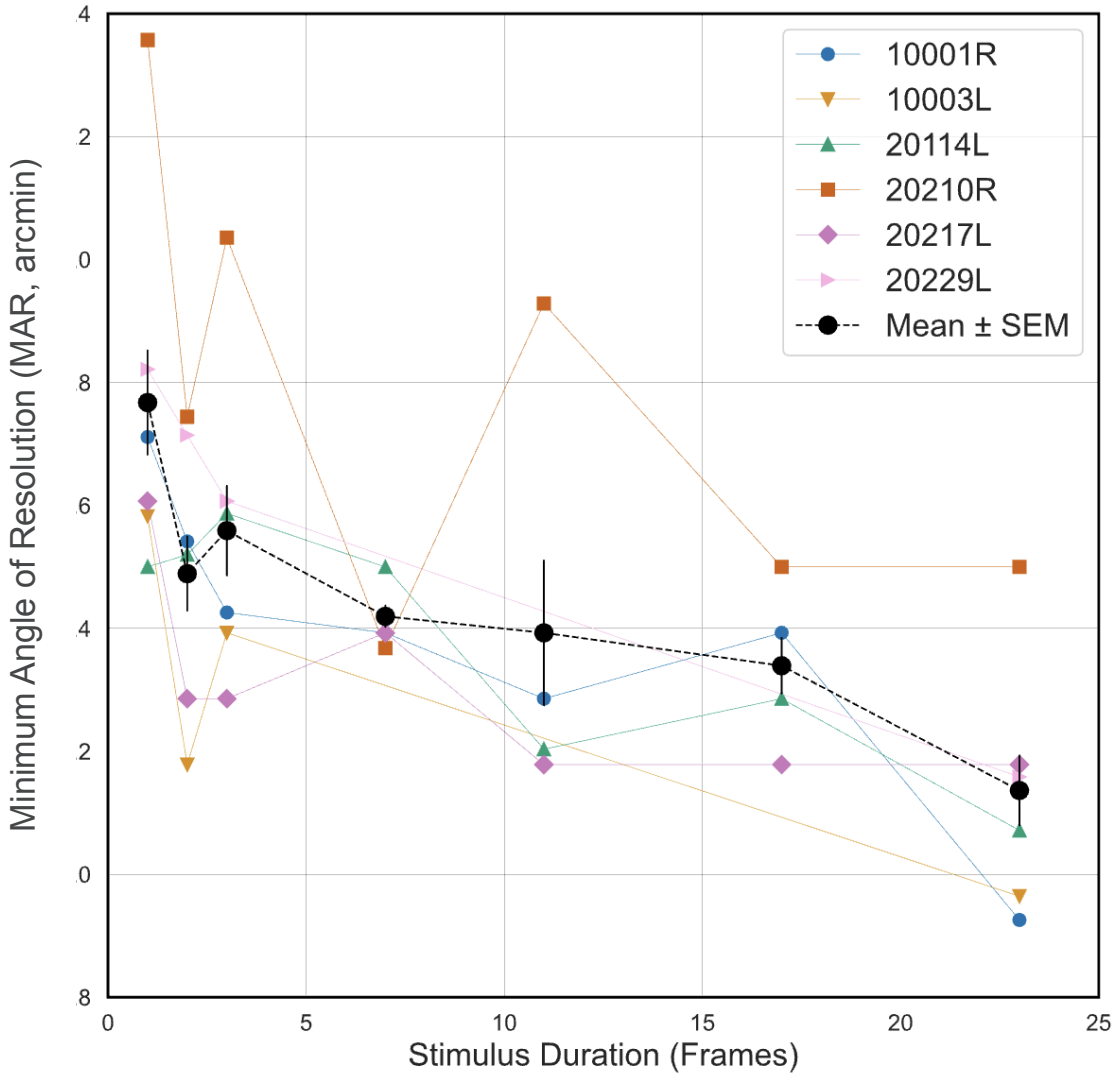


Figure 2.2: Minimum angle of resolution (MAR) as a function of stimulus duration.

roring previous results from Ratnam et al., we show a decrease in performance at longer durations (∼750 milliseconds or 23 frames). However, there are small or no differences at shorter durations from 1 to 11 frames. These results confirm previous findings at longer durations, while also showing that this trend may not hold at shorter durations. The reduction in stabilized performance compared to unstabilized at longer durations is clearly shown (i.e. 17 and 23 frames) for all but 1 subject. At intermediate durations, we see little difference between the FEM removed and natural viewing conditions. At the shortest durations, a slight increase in performance in stabilized viewing is shown. The estimated baseline gain ratio in the absence of stimulus frames is 1.054. A statistically significant negative relationship was observed between stimulus duration and gain ratio (B = -0.007, $p < 0.001$). This suggests that with each additional exposure frame, (i.e., increasing stimulus duration) the expected gain ratio decreases by 0.007. Both intercept and duration effects were found to be statistically significant ($p < 0.001$), affirming the robustness of the observed relationships.

Supplemental Figure A.1 shows the blocked and interleaved (Supplemental Figure A.2) data separately. The blocked design shows a higher performance ratio, meaning that gain 1 trials had higher performance compared to gain 0 at the shortest durations. The interleaved data does not show this same trend. Thus, some effects of fatigue may have been present in the blocked design. Importantly, both data collection protocols show large decreases in performance in the FEM removed (stabilized) condition at longer duration stimulus presentations (> 17 frames). Ultimately, a linear mixed effects model showed the interleaved and blocked data were not significantly different from one another and were combined.

During each frame of stimulus presentation in the AO system, the location of the center of the optotype can be derived, giving the exact movement of the stimulus that is either world or retinally fixed. Figure 2.4 depicts the movement of the stimulus in retinal coordinates for two subjects. Using shifts in location of the stimuli on the retina, we calculated stimulus travel paths for the duration that the stimulus was shown. This can be used to both validate stabilization and compare photoreceptor sampling that occurred in different stimulus gain conditions and durations. To this end, we show trial by trial traces of the stimulus's movement on the retina for two subjects at each duration. The gain 1 traces sample a much smaller portion of the retina compared to gain 0. The increase in spread as the duration increases for gain 1 trials is expected, as stabilizing over a longer period means there is more variability in where the stimulus will be rendered during each frame of stimulus presentation. The natural stimulus sampling of the retina shows a very similar pattern to gain 1 at the 2 frame condition and increases as frame number increases. The longer that a subject has to view a stimulus, the more the eye moves, and the more motion and individual differences in FEM patterns emerges. Subject 10001, for example, has a clear upward tendency to their drift movements.

The area of retina that was stimulated throughout the time course of an unstabilized trial is shown in Figure 2.5. The differences in area in duration conditions are clear – as the eye has more time to make its fixational movements, more of the photoreceptor mosaic samples the stimulus. Supplemental Figure A.3 highlights the difference between the area of retina that is stimulated in the stabilized compared to the unstabilized trials (shown as a

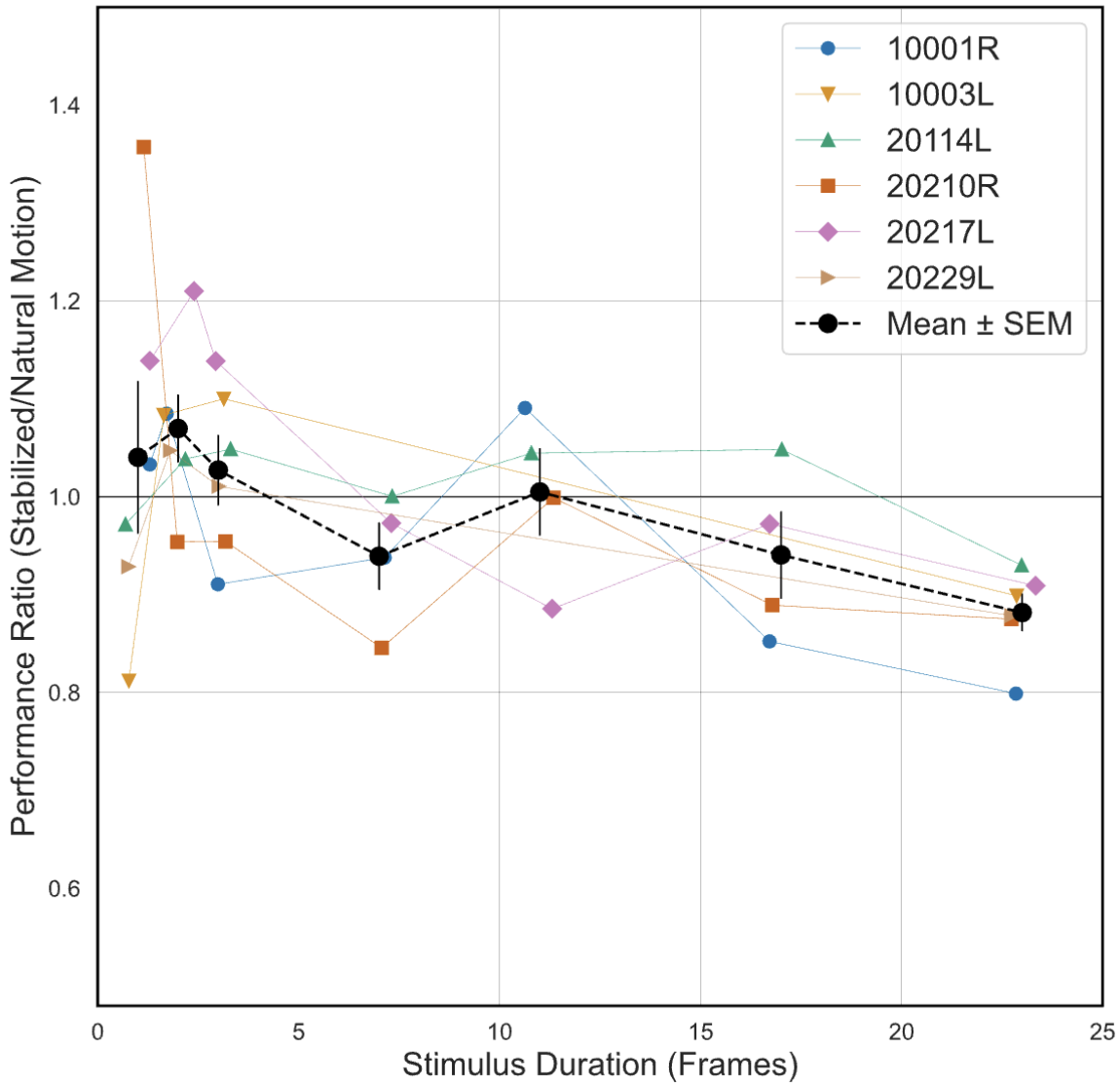


Figure 2.3: Stabilized (gain 1) and unstabilized (gain 0) performance is plotted as the difference between the two conditions, with values above 1 showing better performance in gain 1 condition compared to gain 0. Values along y = 1 represent no difference between these two conditions.

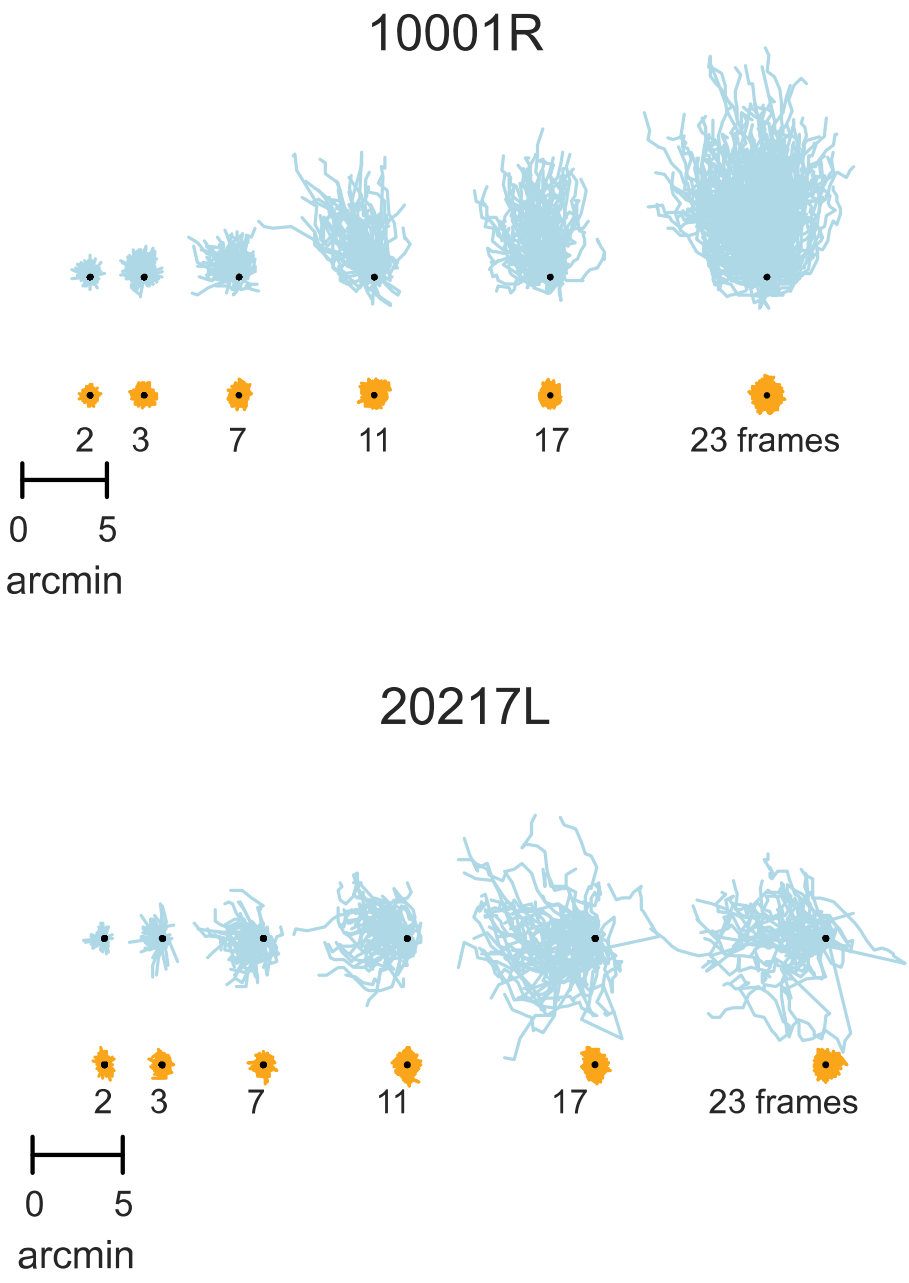


Figure 2.4: Exact stimulus locations were extracted from the position of the E on the retina for each duration. Figure 2.4 shows X and Y shift of the stimulus in a retinally fixed view in stabilized (orange) and unstabilized (blue) trials for subject 10001R and 20217L. Black dots represent the origin point of each trial at (0, 0).

ratio). The ISOA method at 68% was used to measure the stability of the stimulus on the photoreceptor mosaic. Longer stimulus durations led to more retinal area sampled, which is restricted in the stabilized condition. Thus, any variations in acuity from the stabilized to the unstabilized conditions should in some part be explained by this discrepancy in sampling area.

Figure 2.6 dissects the unstabilized data into either high or low motion (relative to the median) for each subject and depicts normalized unstabilized performance for each subject and each duration. Durations 2 and 3 show a slight but insignificant bias towards trials with less motion having better performance. Paired t-tests revealed non-significant differences in performance between the below and above median conditions for 2 ($t(DF) = 1.97$, $p = 0.11$) and 3 frames ($t(DF) = 0.73$, $p = 0.50$). However, across longer stimulus durations, the opposite (but still insignificant) pattern emerges (23 frames ($t(DF) = -1.78$, $p = 0.14$)). For longer stimulus durations, trials with relatively more motion for each individual subject generally had higher performance (with the exception of one subject). This is in contrast to the no retinal motion (stabilized) condition, plotted in orange, where no benefit was seen between relative eye movement bins.

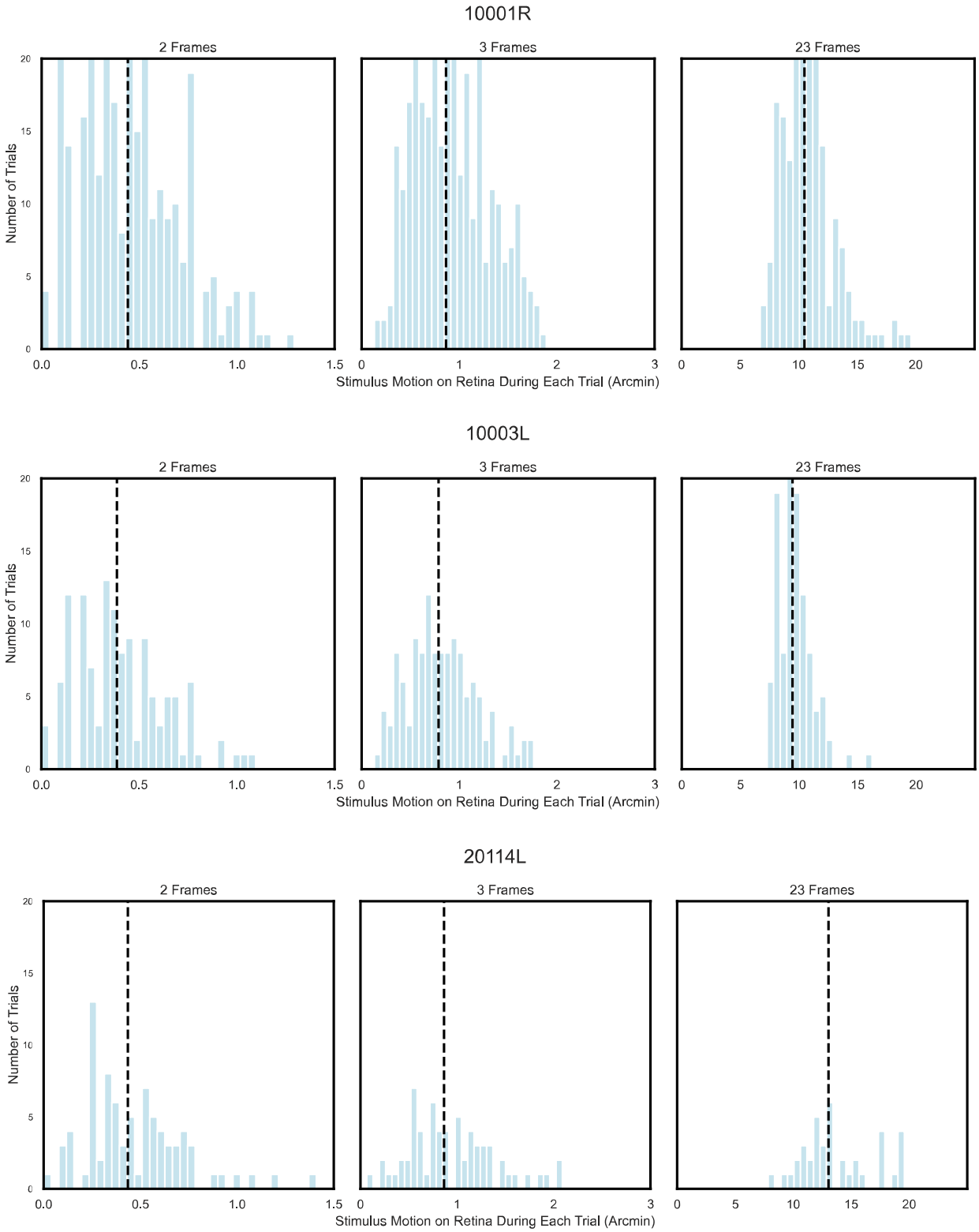
2.4 Discussion

Impact of Duration on Retinal Stabilization

Our findings closely align with those of previous investigations showing that stabilized acuity is worse compared to when the eye is allowed to sample a stimulus naturally. However, it is crucial to better understand how this modulation varies based on the specific temporal characteristics of a stimulus. In our investigation, the stimulus is shown on a relatively low persistence stroboscopic display compared to others. During each frame, the E is displayed line by line over a small portion of a .9 degree field. One explanation for the relatively lower deleterious effects of stabilization (compared to other investigations) could be because the AOSLO stimulates with a temporal envelope applied to a stimulus. Even though the stimulus is stabilized on the photoreceptor mosaic, brief, low frame rate presentations might introduce other temporal dynamics that undermine the effects of stabilization and restores some fine spatial acuity.

The Effects of Fixational Eye Motion at Short Compared to Long Durations

A critical aspect of image stabilization is the time course over which we stabilize a stimulus. Previous investigations have generally only examined stabilization at longer durations (Ratnam et al., 2017; Rucci et al., 2007). Here, we show that at shorter durations, the effects of removing retinal motion do not impact performance. While this has been predicted by computational work (Anderson et al., 2020), it has yet to be fully explored in the human eye.


10001R
2 Frames
3 Frames
23 Frames
Number of Trials
Stimulus Motion on Retina During Each Trial (Arcmin)
10003L
2 Frames
3 Frames
23 Frames
Number of Trials
Stimulus Motion on Retina During Each Trial (Arcmin)
20114L
2 Frames
3 Frames
23 Frames
Number of Trials
Stimulus Motion on Retina During Each Trial (Arcmin)

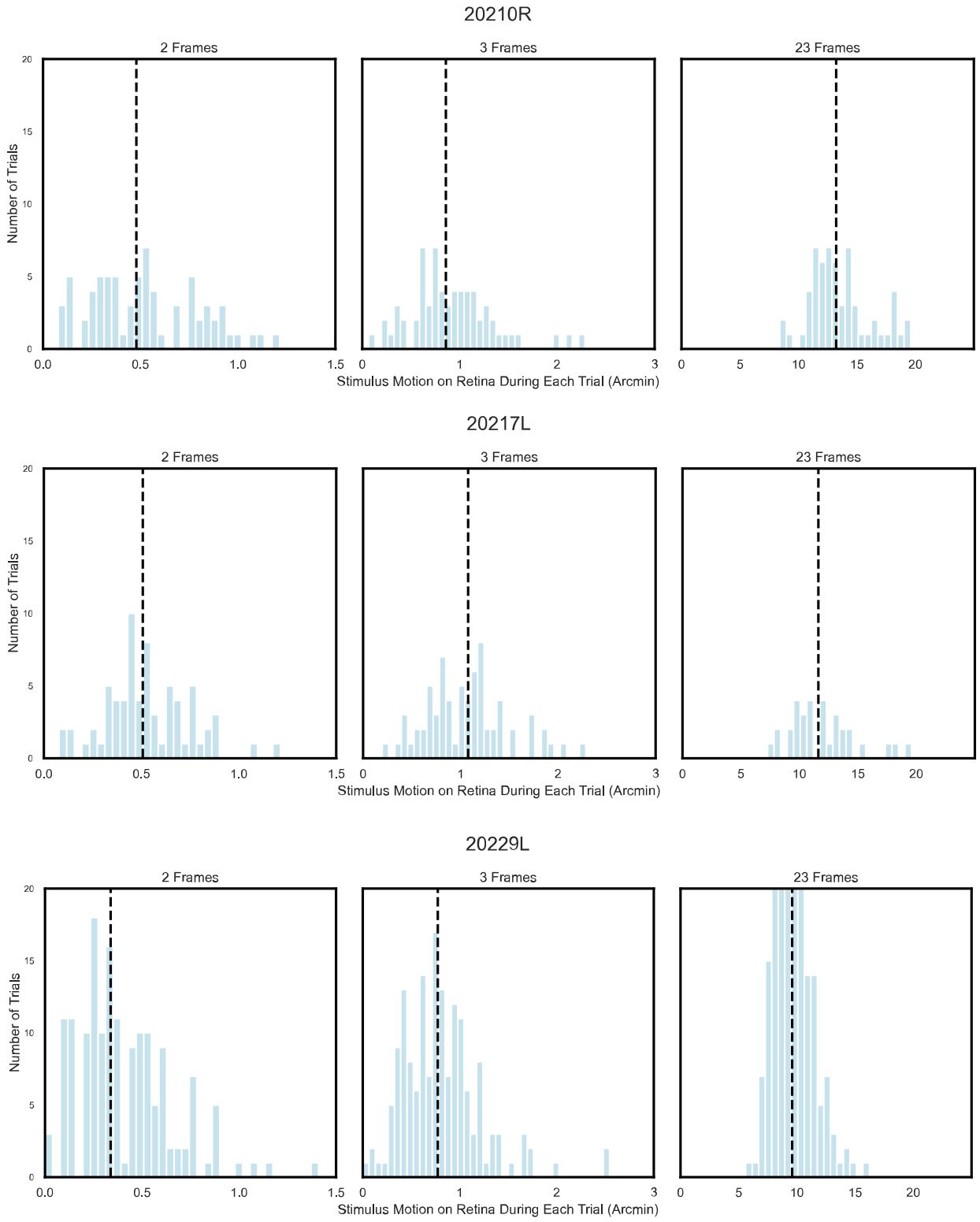


Figure 2.5: The average travel path of a stimulus on the retina during each unstabilized trial. Each panel shows the amount of motion for 2, 3 and 23 frame stimulus duration for each individual subject. The median motion is plotted with a dashed line. Note the difference in X-scale across columns.

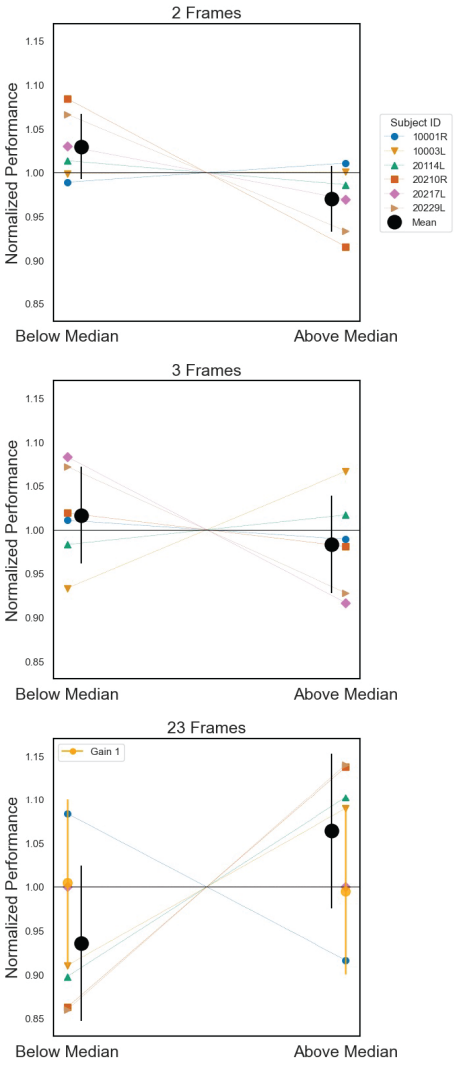


Figure 2.6: Performance (normalized to overall percent correct) for each subject on unstabilized trials with more or less motion than the median for 2, 3 and 23 frames of stimulus presentation.

A critical aspect to the growing literature on intersaccadic fixational eye movements is the temporal window in which a stimulus is allowed to be sampled. Put simply, the eye needs time to make fixational movements. As more time passes (during which drift and tremor occur), the eye moves farther from its origin point until it is displaced by a saccadic movement. Thus, attempts to model motion's effect on spatial vision must depend on elapsed time. Assuming a stimulus is world fixed, this means that the eye also samples a stimulus more over time. If the eye fails to move during an elapsed time interval, a stimulus is effectively stabilized on the retina. As it relates to our experiment, the difference between a stabilized and unstabilized stimulus presentation is only meaningful given a large enough temporal window of stimulus presentation. Thus, it is critical to categorize the differences in retinal sampling in these two conditions over time. We see that there is little difference between retinally and world fixed performance on a fine spatial acuity task at short enough timescales. Most intersaccadic fixational periods are interrupted by 2-3 microsaccades per second (Rolfs, 2009; Rucci & Poletti, 2015). At this 200-300 ms timescale, our results suggest that the benefits of fixational eye movements are not seen in natural fixation. The positive effects of only drift and tremor motion on acuity are outside of the time course of normal vision.

Additionally, this effect is dependent on the relative motion that occurs during each trial. Differences over time will be exacerbated by drift and tremor velocity, both of which vary by individual (Bowers et al., 2021a; Cherici et al., 2012). Other effects of individual differences will not be examined here, as variations in eye movement patterns can significantly influence visual encoding. For the purposes of our investigation, in order to remove individual variation in fixational stability, we isolated inter-individual differences in movements on a trial-by-trial basis. Previous work suggests that drift velocity on an individual trial plays an important role in performance on a fine acuity task (Clark et al., 2022). Trials with less motion (for that subject) had a higher proportion correct on an acuity task at 500ms. In conflict with Clark et al., our results show that within subjects, those trials with more than average motion for an individual generally had higher performances compared to trials with less than average motion in longer stimulus presentations. Importantly, this difference was not seen at short timescales, where the eye did not have time over which to make fixational movements. The discrepancies seen between our investigation and that of Clark et al. may be due to a number of differences in experimental design. First, our stimuli were consistently smaller than that used in Clark's work (0.5-4 arcmin, see Figure 2.2 for our stimulus sizes by duration). At this level of granularity, the differences in benefits seen from single-cone resolvable compared to larger stimuli might change the way that FEM reformat spatial information. In addition, Clark and colleagues used a 500ms stimulus presentation. We show in Figure 2.3 that the effects of retinal motion are dependent on the duration. Therefore, the duration of a stimulus's presentation may cause a large discrepancy in findings. Another possible reason is that using the median in our analysis in Figure 2.6 may obscure the actual amount of eye motion that occurred, which may help explain our opposing findings. Lastly, our stimulus delivery protocol for stabilized trials were contingent on subjects carefully fixating, thus our subjects may have been more motivated to steadily fixate. In post processing, we also employ

a strict trial exclusion criteria, which may have introduced a sampling bias for trials where the eye was exceptionally still. While our data are not statistically conclusive, future studies may aim to further examine the relationship between fixational stability and performance at various stimulus sizes and durations on an individual basis, where small idiosyncrasies may lead to large differences in perception.

2.5 Conclusion

In conclusion, our study not only reinforces the findings of previous research but also sheds light on crucial aspects of fixational eye movements and their effects on fine spatial acuity. Our results confirm that stabilization leads to a modest impairment to fine spatial acuity, particularly for stimulus durations of approximately 23 frames (or roughly 750 milliseconds). Additionally, we show that this effect is time-dependent, and decreases with shorter durations of stimulus presentation. Without sufficient time for intersaccadic eye movements to occur and influence downstream visual processing, they are not beneficial to acuity. This understanding of fixational eye movements not only helps to psychophysically explain existing computational models of FEM, but also adds to the broader understanding of the function of fixational eye movements. Specifically, any effects of these movements are contingent upon the duration over which they can move the photoreceptor mosaic. Our findings highlight the temporal aspect as a critical determinant of their influence. When taken together with the growing body of literature studying unstable fixation, this study informs our understanding of how the eye's drift and tremor movements impact fine spatial acuity and, in turn, influence visual perception.

Chapter 3

The Effects of Direction and Feature-Specific Imposed Retinal Motion on Fine Spatial Acuity

3.1 Introduction

The eye's smallest movements – drift and tremor – are critical for fine spatial vision. However, the full extent of fixational eye movement's (FEM) impact on human perception are not well understood. When we remove the effects of fixational eye movements in a laboratory setting, there are deleterious effects on visual acuity. One line of work uses adaptive optics scanning laser ophthalmoscopy (AOSLO) to lock a stimulus onto one patch of photoreceptors. This is achieved by simultaneously tracking the eye's changes in position over time and mirroring these movements in the real world to compensate for any displacement that might occur from the natural fixational movements (Stevenson et al., 2010). When a stimulus is 'stabilized' so that the effects of drift and tremor are eliminated, performance decreases on acuity tasks when compared to natural viewing (Ratnam et al., 2017). While this area research has been of interest for decades, the full extent of the conditions in which these movements are helpful or harmful have still not been explored.

The current literature posits two main benefits from natural fixational retinal image motion. First, computational work has suggested that FEM help sample fine stimuli that are under-sampled by the photoreceptor mosaic (Anderson et al., 2020). Thus, if the eye is allowed to move naturally, the dynamic signal encoded by the cone mosaic enables the resolution of a stimulus that would be indiscriminable under static viewing. Specifically, this model emphasizes the benefit of eye movements near the spatial resolution limit of the cone mosaic (Rossi & Roorda, 2010). Second, fixational movements may serve to whiten inputs – amplifying high spatial frequency information passed from the retina to the cortex to aid in the perception of fine detail (Boi et al., 2017). Critically, these effects depend on the spatial frequency of the visual input, the magnitude of eye motion, and the temporal dynamics of

light encoding. Human psychophysical work shows that medium (11 CPD) spatial frequency information is affected by stabilization, but not low (4 CPD) spatial frequency gratings (Rucci et al., 2007).

Not only do the benefits of fixational eye movements depend on the spatial frequency of the stimulus, but they also depend on how those stimuli are oriented relative to the direction they are moving on the retina. Previous studies have found that eye movements stabilized selectively either parallel or orthogonal to a stimulus's grating orientation can have very different impacts on acuity. On an orientation discrimination task using 5-11 cycle per degree spatial frequency gratings presented for 1 second, motion orthogonal to the grating orientation was critical for performance (Rucci et al., 2007). This interaction between fixational eye movements and stimulus feature orientation has yet to be fully studied in relationship to discrimination. While we understand that the eye's movements are important for fine spatial acuity, we do not yet have a full understanding of the kinds of motion that are critical for the benefits and detriments obtained from natural motion.

An important consideration in this line of work is the individual differences in drift and tremor. When the eye is allowed to naturally drift, there are large differences in both span and directional tendencies of these movements (Cherici et al., 2012). These also depend on task demand and target (Bowers et al., 2021a). While individual differences in FEM direction and magnitude's resulting consequence on visual acuity are becoming a subject of current interest in the literature (Clark et al., 2022), this investigation seeks to understand only the effects of motion relative to a stimulus's features. Thus, we have taken the otherwise individualized motion patterns and standardized them, carefully imposing various amounts of retinal motion to uncover what the effects are on acuity. This can be accomplished by using the AOSLO, which has multiple advantages, including highly sensitive validation of stabilization and stimulus trajectory. Critically, the AOSLO is also able to impose a predefined magnitude and direction of retinal motion on top of the movement necessary for stabilization.

Many factors, such as magnitude and direction, will change the way that a stimulus is sampled by photoreceptors, potentially leading to different percepts, and ultimately affecting performance on acuity tasks. First, the magnitude of motion is critical. The photoreceptor mosaic has a temporal integration window that places an upper limit on the temporal frequencies that can be transduced and relayed to the brain (Baudin et al., 2019; Horwitz, 2020). As a consequence of when the magnitude of a stimulus's motion is too high, motion blur can occur (Burr, 1980; Westheimer & McKee, 1975). This can lead to unresolvable blurring dependent on contrast and spatial frequency, but is mostly dictated by instantaneous velocity (Derrington et al., 2004). On the other hand, if a stimulus is completely stationary on the retina, visual fading occurs (Tulunay-Keesey, 1982), rendering an image completely invisible over time. While there is some work which posits that natural drift motion is not optimal for fine spatial vision (Ağaoğlu et al., 2018; Clark et al., 2022), a balance between too much and too little motion must exist. Second, the direction of movement is also a critical component to how resolvable a stimulus is to the human visual system. For example, if a horizontal bar is shown, the retinal sampling patterns will vary considerably depending

on if the bar's movement is horizontal or vertical. Over time, vertical motion will create the summed image of a square, while horizontal motion creates a long horizontal line. Clearly, a subject's performance will be affected by this type of difference in motion when asked to discriminate between these two stimuli. Last, the interplay between magnitude and direction may also play a role in visual acuity. An object that moves more quickly and whose stimuli are also more blurred because of the orientation of its features should be more difficult to resolve. Thus, we expect both the magnitude and direction of stimulus motion to have different effects on human visual acuity. This study aims to further investigate the role of motion blur induced by drift and tremor by imposing predetermined motion on the retina, further controlling the effects of FEM and their relationship to performance on a fine visual acuity task.

3.2 Methods

Participants

Five subjects (two male, three female; ages 26-39) with no known retinal disease were included in this experimental data collection protocol. Informed consent was granted from each subject and all procedures adhered to the Declaration of Helsinki.

Apparatus & Stimuli

A more detailed description of the system is included in the methods section of Chapter 2. At a high level, we used an adaptive optics scanning laser ophthalmoscope to present gaze-contingent stimuli to targeted areas of the photoreceptor mosaic (Roorda et al., 2002; Wang et al., 2019). Subjects were dilated and asked to use a bite bar to hold their head steady. Infrared light for imaging (wavelength: 840 $\pm$ 25 nm; luminance: approximately 4 cd/m^2) and wavefront sensing (wavelength: 940 nm) was filtered from a supercontinuum laser source (SuperK Extreme; NKT Photonics, Birkerød, Denmark). A wavefront sensor and deformable mirror worked together to remove higher order optical aberrations. Ultimately, a 30 Hz 512 $\times$ 512 pixel image was used for all analysis. The square imaging raster subtended 1.4 degrees or 0.164 arcmin per pixel.

Chapter 2 includes specifics of stimulus presentation and retinal image delivery. Briefly, the AOSLO laser was modulated to produce a negative contrast 4-AFC tumbling E optotype on a dim red square. Using a gamepad, subjects reported tumbling E gap direction. We presented either natural, stabilized or imposed motion onto these optotypes (Figure 3.1a). Trials in which the stimuli's position moved in the world in order to stay on the same patch of photoreceptors throughout a trial are called 'stabilized' or have a gain of 1 in relationship to the eye's natural movement. The imposed motion trials were also stabilized to account for individual differences (Figure 3.1a). Trials that stayed unmoving in world fixed coordinates were 'unstabilized' or had a gain of 0. An E was rendered for only a portion of the 30 Hz frame (see Figure 3.1b). We use frames to more accurately describe the duration of

each stimulus presentation, as well as durations to help compare our findings to previous investigations (Ratnam et al., 2017).

In the additional motion conditions, we randomly interleaved an imposed motion of 0.5, 1 and 2 bar widths in random cardinal directions onto the optotypes (Figure 3.1c). These shifts in position were presented over 3 frames, where the bar width was shifted by the imposed motion condition per frame (Figure 3.2). The stimuli are rendered over time in the AOSLO, and thus are presented for approximately 70 ms. The magnitude and direction of the stimuli on the retina can be used to verify our imposed motion and stabilization techniques (see Supplemental Figure B.1). These traces are derived from the stimulus trajectory via the images of the stimuli on the photoreceptor mosaic taken from the AOSLO.

Experimental Procedure

In this study, stimulus motion was imposed on the retina to characterize its effect on observers' ability to identify the orientation of a tumbling-E optotype. Stimuli were shown for ∼70ms (3 frames) following the same methods described as before, a duration for which previous experiments suggest motion blur may limit performance for high spatial frequency targets (Packer & Williams, 1992). Stimuli were shown both unstabilized and stabilized on the retina. Additionally, the optotypes were stabilized and moved in a predetermined direction labeled as either parallel or orthogonal (Figure 3.1c) to the orientation of the stimulus. We aimed to test how the interplay between different stimulus features and imposed motion magnitudes influenced performance on an orientation discrimination task. As shown in Figure 3.1e, the summed retinal image over the course of the 3-frames of one trial will result in very different stimuli when viewed over time. Stimulus motion trajectories were varied in magnitude relative to the MAR of the individualized stimulus size.

These magnitudes included half, one bar and two bar widths of the tumbling E optotype. This imposed motion in addition to retinal stabilization was shown over three frames at 30 Hz. All stabilization, motion magnitude, and motion direction conditions were randomly presented within 16, 90 trial blocks after a 40 trial Quest staircase procedure to find an unstabilized stimulus threshold of 80% in 5 subjects. Trial rejection was done similarly to Chapter 2, with both automated and manual review of trials.

3.3 Results

Similar to previous investigations (Ratnam et al., 2017) and Chapter 2, we compared natural motion to stabilized performance. The means across subjects for each duration on unstabilized trials varied from 71-95%, with an overall mean performance of 81%. Means on stabilized trials varied from 76-82% with a mean of 78% across subjects. Individual subject and group mean performance on stabilized and unstabilized performance is shown in Figure 3.2. A paired t-test revealed there was no statistical difference in performance between these two conditions. This mirrors results shown in Chapter 2, specifically that there is no

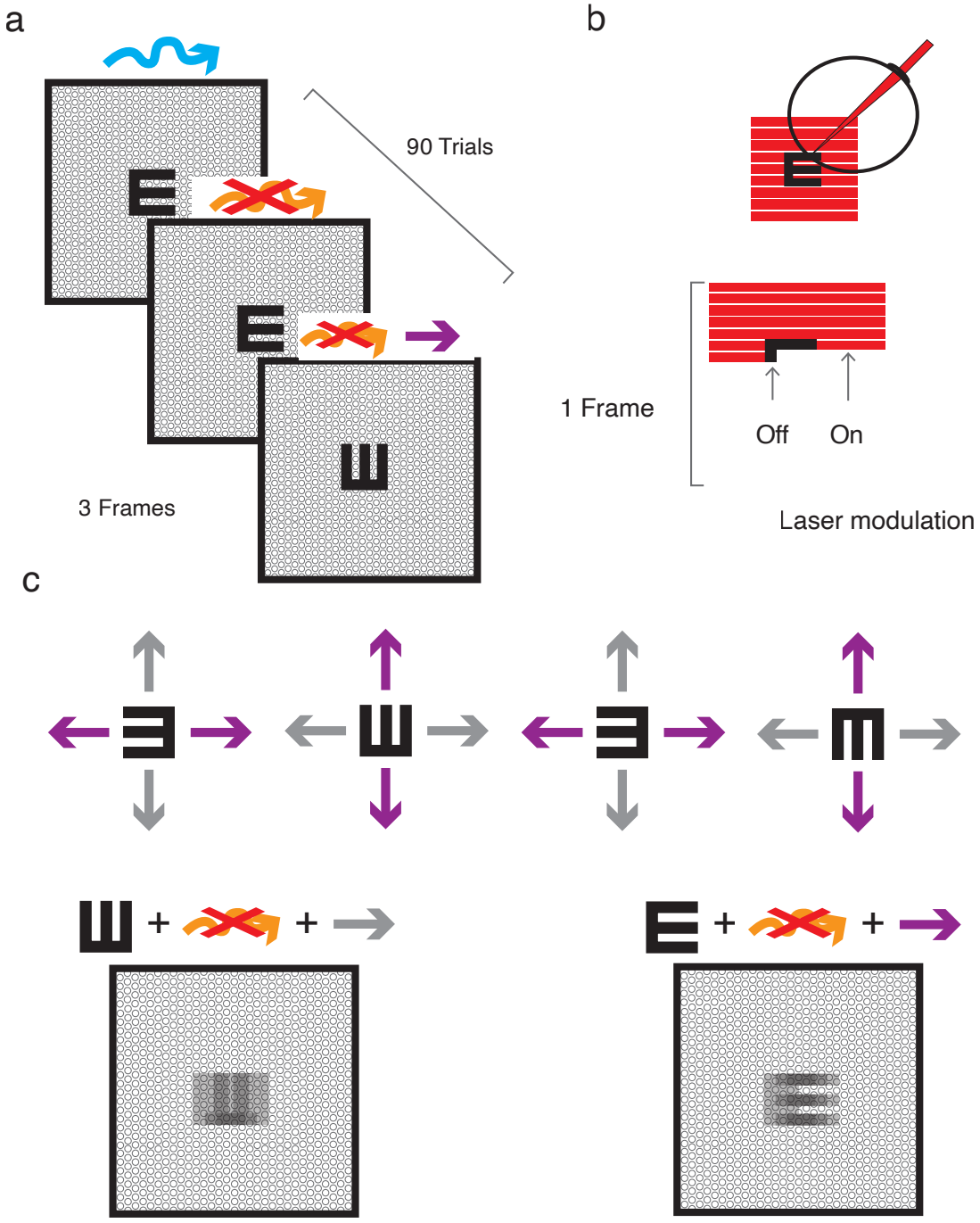


Figure 3.1: a. Within 90 trials, we compared stabilized (n = 15) and unstabilized (n = 10) performance. The remainder of trials were imposed motion. b. Subjects saw a 1.4 degree red field with a negative contrast stimulus made by modulating the laser as it scanned the retina. c. These imposed motion trials were separated into 3 motion categories – 0.5, 1 or 2 widths of optotype bar motion per frame. All stimuli were shown for 3 frames, meaning that the final motion was either 1.5, 3 or 6 bar widths from the original location of presentation on the retina. Critically, these trials were also stabilized on the retina, meaning that the only sampling of the photoreceptor mosaic was due to the imposed motion, not the eye's natural movements. Trials were divided into parallel (purple) or orthogonal (gray) motion. The image summation in this figure is occurring in retinotopic coordinates. This distinction separates critical downstream effects to the final summed image presented to the retina.

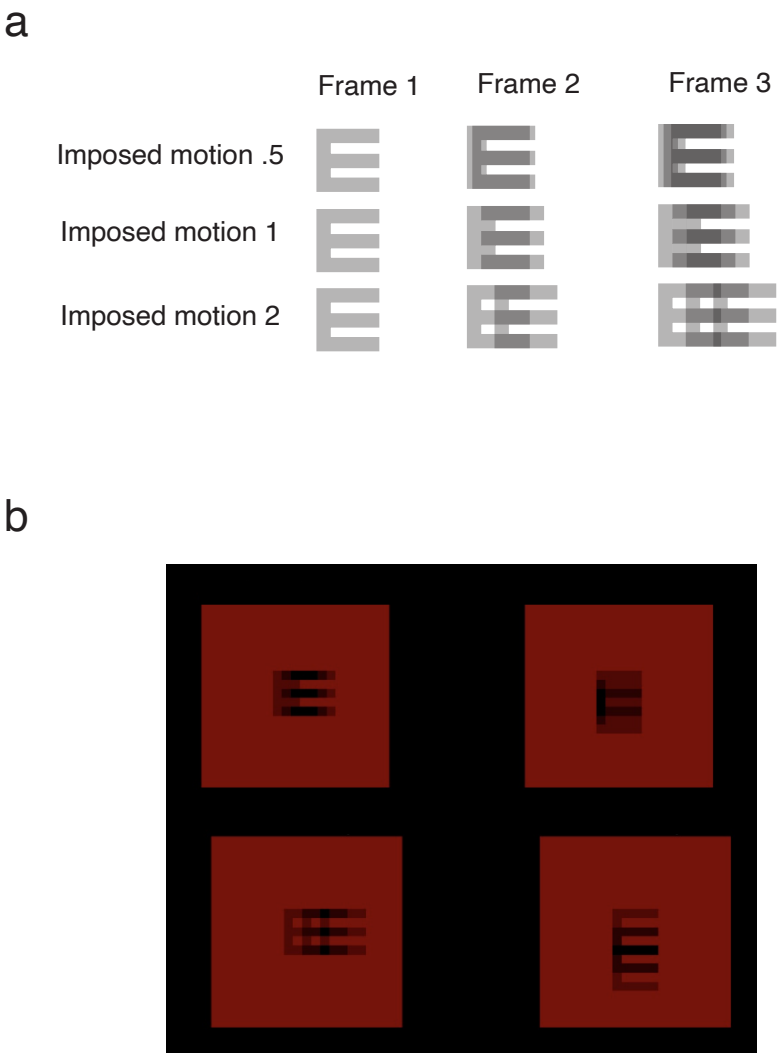


Figure 3.2: a. A depiction of the summed retinal image of the optotypes over a 3-frame stimulus presentation as viewed by the subject in the AOSLO. The imposed motion conditions can be divided into either parallel (left column) or orthogonal (right column) motion. This distinction is relative to the critical features of the optotype (the bars). For example, a rightward facing E moving to the right would be considered a parallel trial, whereas the same stimulus moving upwards would be considered an orthogonal motion trial. b. In a simple graphic showing the relationship between stimulus orientation and motion, the importance of this distinction is clear. Depending on the temporal integration window that each individual photoreceptor may pool over, the parallel and orthogonal summed images may create very different percepts. This may lead to a reduction in discrimination, leading to decreased performance.

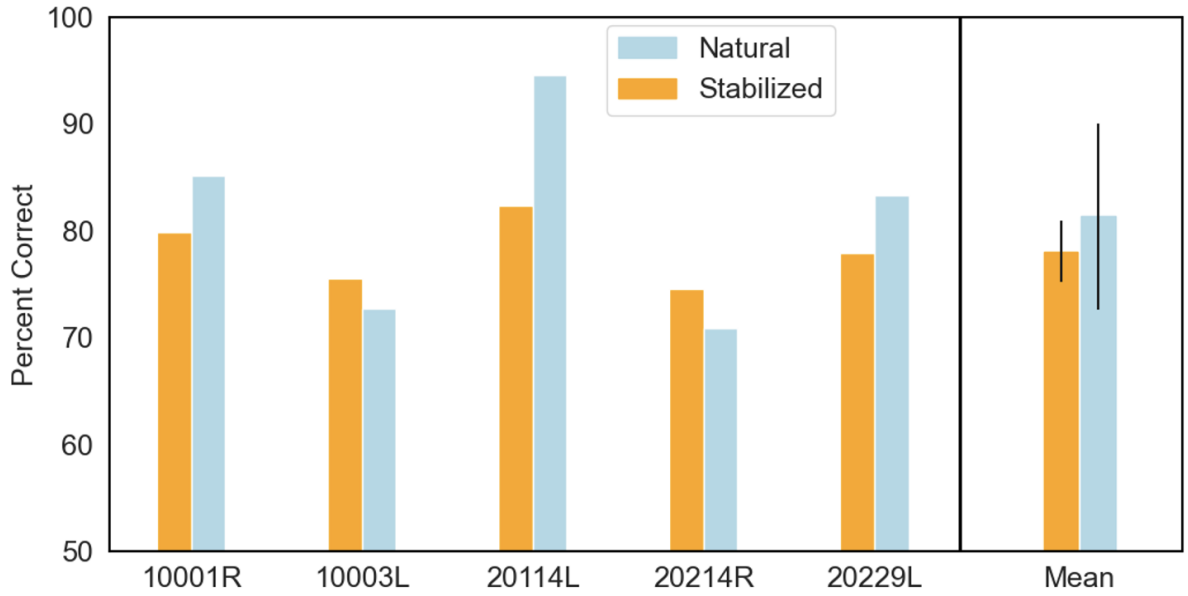


Figure 3.3: As in previous investigations, we compared natural and stabilized (retinal motion removed) performance on a 4-AFC tumbling E task. Paired individual performance is shown on the left, with overall mean performance ± 1 standard error of the mean (SEM) on the right. Chance is at 25% (not shown). Natural performance was used to select individual stimulus sizes at 80% performance.

difference between stabilized and unstabilized performance at short durations (3 frames). In fact, for two subjects (10003L and 20214R), stabilized performance is slightly better than natural motion.

Next, we compared motion type relative to critical stimulus features across imposed motion conditions (see Figure 3.2a and 3.2b for representations of the summed stimuli projected onto the retina). Figure 3.4 shows the difference in percent correct (normalized by individual performance on gain 1 trials) across various motion direction and velocities. Values above 1 indicate performance better than stabilized, while those below 1 indicate impaired performance compared to stabilized trials. Gain 0 performance is again not different from performance on the gain 1 condition (see Figure 3.3). Critically, there are key differences in performance between the parallel and orthogonal conditions.

Paired t-tests were conducted to compare the parallel and orthogonal motion patterns between various imposed motion values. The t-test results indicated potential significance in the imposed motion condition of 1 ($t = -1.975$, $p = 0.084$), suggesting a trend towards a difference between the two conditions. However, no significant differences were observed at imposed motion of 0.5 ($t = -1.357$, $p = 0.212$) and 2 ($t = 0.432$, $p = 0.677$). After applying the Bonferroni correction to account for multiple comparisons, the corrected p-value for the imposed motion of 1 remained relatively low (0.335), indicating a potential trend, however none of the corrected p-values reached the adjusted significance level of 0.05. These findings suggest that further investigation with a larger sample size may be necessary to confirm the

observed trend.

Figure 3.2a provides a representation of the difference between what is projected onto the retina during the parallel and orthogonal conditions at this imposed motion value. In addition, we see in Figure 3.4 that stabilized performance has the highest normalized percent correct. This is consistent across all imposed motion conditions, as well as the normal retinal motion condition. Thus, we find that motion is never helpful under the conditions studied here.

Next, we examined the underlying trends in response errors which drive these results. In Figure 3.5, we examined the proportion of making a 180-degree compared to a 90-degree error. A 90-degree error is a misreporting by a subject of 90 degrees from the stimulus orientation that was shown (e.g. reporting left when orientation was up), whereas a 180-degree error is a response in the opposite direction of the stimulus (i.e. saying down when the stimulus is facing up). By chance alone, we would expect approximately one-third of errors to be 180-degree errors and two-thirds to be 90-degree errors. However, a slight bias towards 180-degree errors is indicated by the black dot, suggesting that participants are more likely to perceive the stimulus as being oriented horizontally or vertically rather than obliquely. This bias is further accentuated when parallel motion is imposed, as shown by the purple dots. Notably, orthogonal motion produces a different pattern of errors, particularly evident at the imposed motion of 1 condition, where participants predominantly make 90-degree errors. This suggests that the orthogonal motion condition, especially at an imposed motion of 1, presents unique challenges to discrimination, potentially due to the interaction between motion and orientation. This may be a result of smearing that occurs from the orthogonal bars, as parallel motion would not induce the same kind of blurring with motion.

Figure 3.6 depicts the proportion that a subject guessed the motion as the orientation of the E (chance = 25%). Subjects were most likely to make this type of error during the imposed motion of 1 condition when the movement of the optotype was orthogonal to its features. The mean response rates for the parallel motion conditions did not significantly differ from the expected chance level of 25% across imposed motion conditions: 0.5 ($t(7) = -0.45$, $p = 0.677$), 1 ($t(7) = -2.09$, $p = 0.104$), and 2 ($t(7) = 0.21$, $p = 0.841$). Similarly, for the orthogonal motion conditions, no significant differences were found for imposed motions of 0.5 ($t(7) = 0.39$, $p = 0.717$) and 2 ($t(7) = -0.85$, $p = 0.444$). Critically, a significant and above-chance difference was observed for orthogonal motion trials with an imposed motion of 1, where the mean response rate ($M = 0.43$, $SD = 0.08$) exceeded chance, $t(7) = 5.29$, $p = 0.006$. This is surprising because these errors do not increase with higher magnitude. The 2 bar imposed motion condition saw chance level 'orientation-motion' errors. This suggests the effect of ambiguity was more pronounced only from the interaction between both velocity and stimulus features, and that this effect might be more important to fine target discrimination than magnitude alone.

Lastly, we investigated the stimulus motion's relationship to the gap direction of the optotype (Figure 3.7). We divided trials with motion that was either toward (0 degree) or away (180 degree) from the stimulus orientation, and therefore only included parallel trials. A decrease in acuity may show that for example, a horizontally oriented bar might

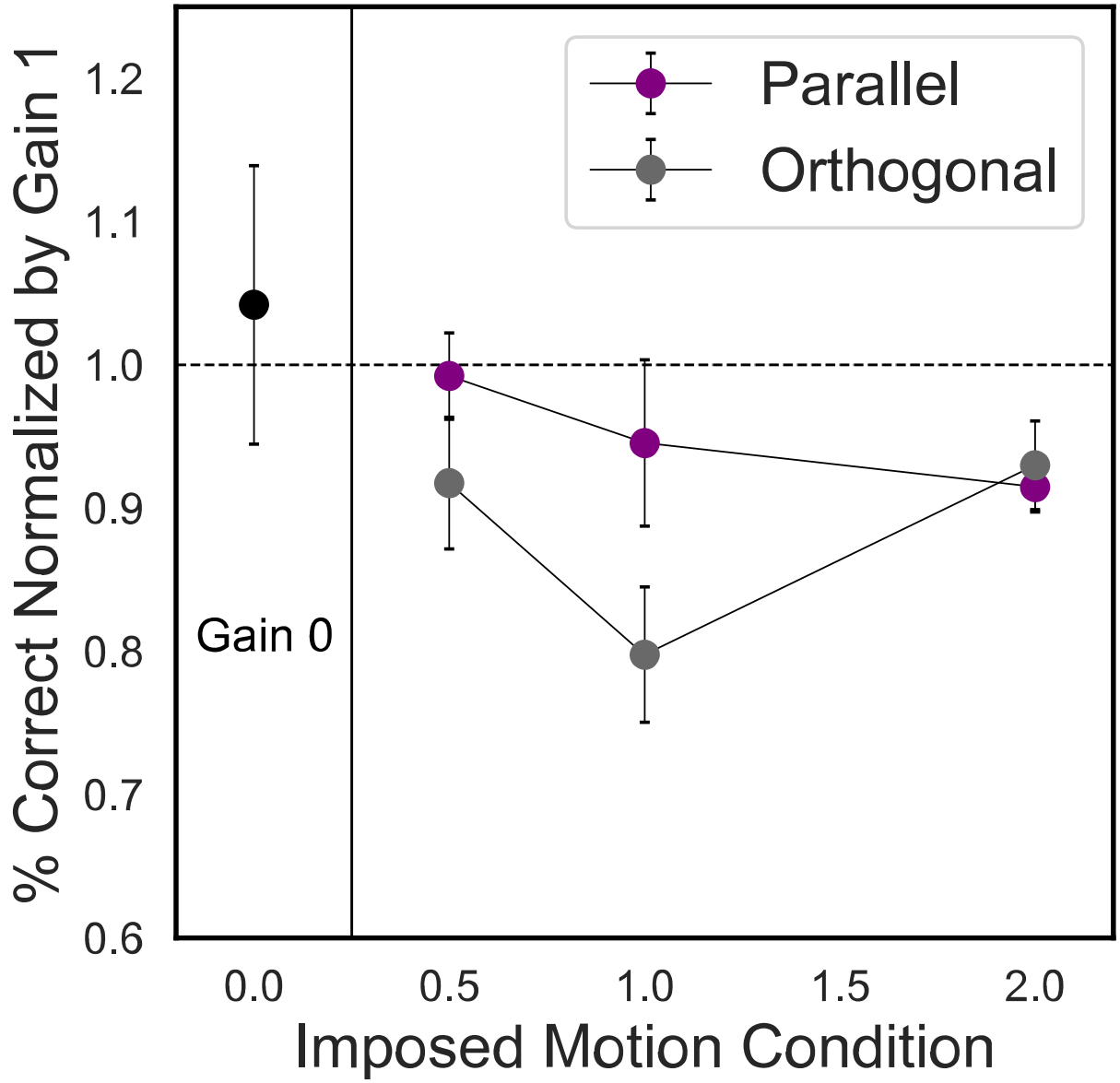


Figure 3.4: Figure 3.4 shows the performance on various motion conditions across all subjects ±1 SEM. All performance is normalized by individual stabilized (gain 1) performance. Parallel and orthogonal motion from the stimulus's critical features are shown separately. See Figure 3.2 for graphical representations of the summed retinal images.

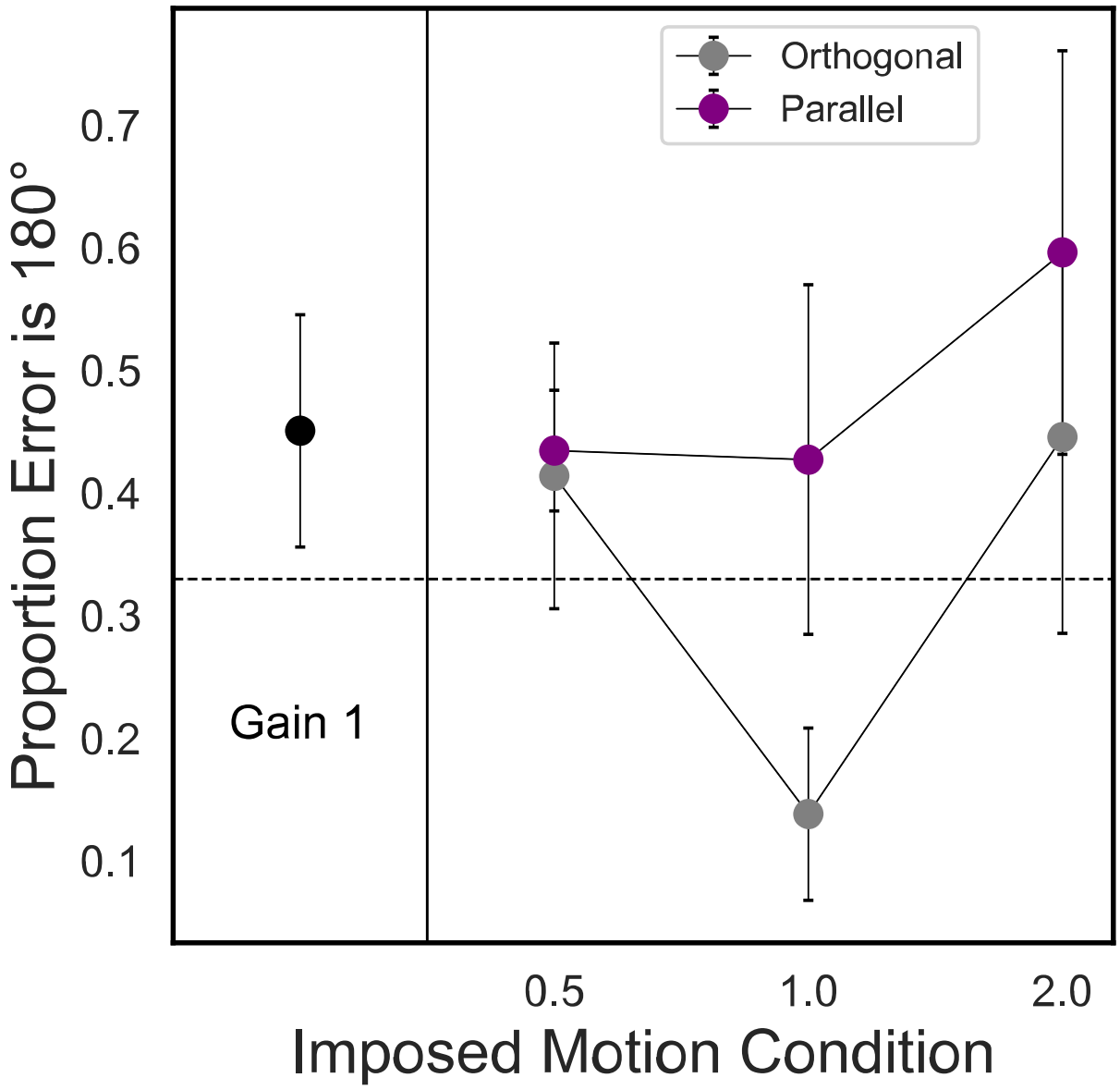


Figure 3.5: The proportion a subject made a 180 compared to a 90 degree error when incorrectly responding to stimulus orientation. Data points have been averaged across all 5 subjects. The chance of making a 180 degree error is 1/3, marked by the dashed horizontal line.

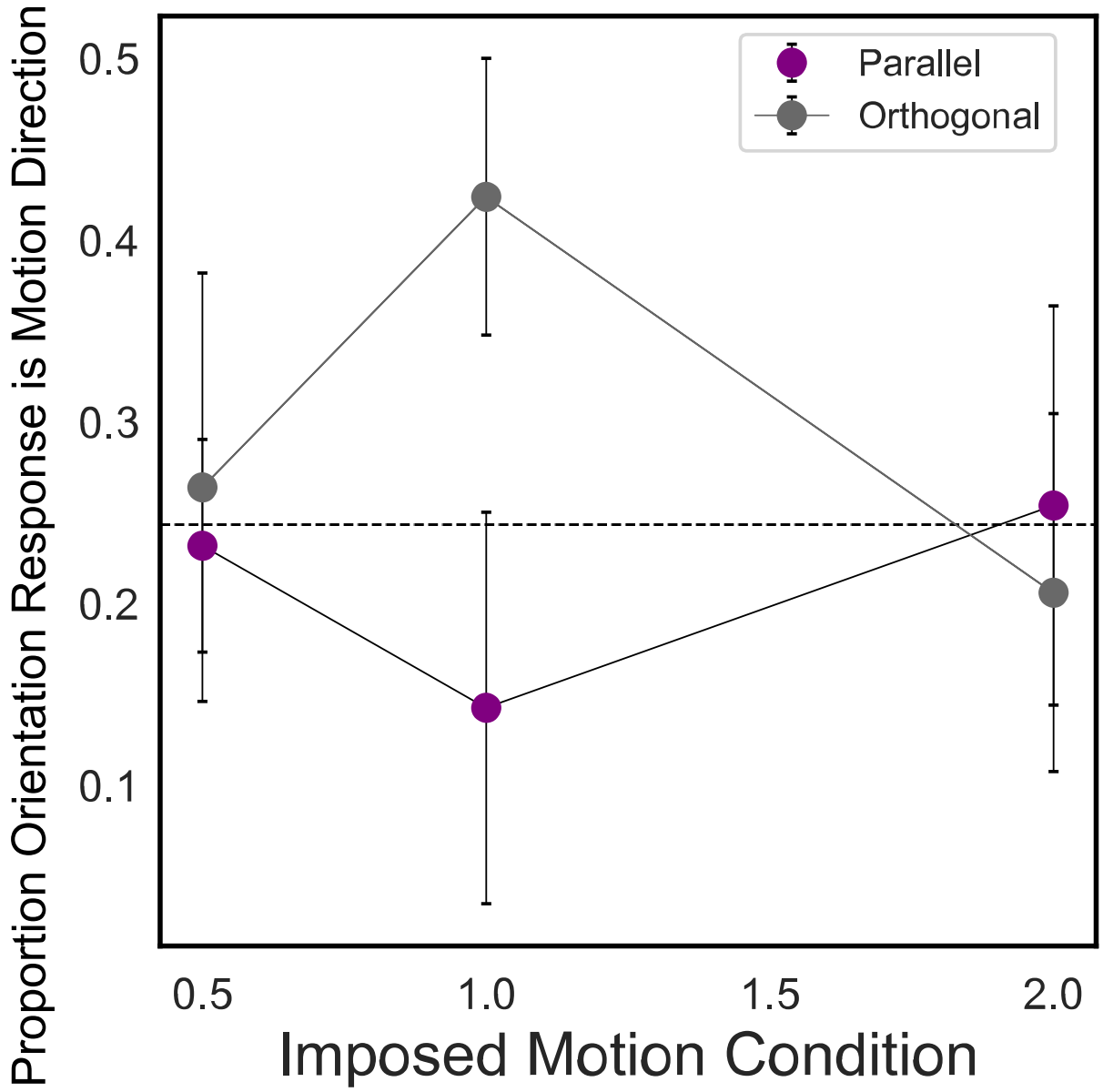


Figure 3.6: Figure 3.6 shows the proportion subjects responded the direction of imposed motion for the orientation response for incorrect trials. Chance level is 25% (horizontal dashed line). Both parallel and orthogonal motion conditions are shown, along with different imposed motion values. The values shown here reflect the mean (±1 SEM) across subjects that an incorrect response was the motion direction.

disrupt processing if it is integrated as overlapping with vertically oriented features over time. While a visual inspection of the plotted data suggests a potential downward trend in both the orthogonal and parallel conditions with more imposed motion, the results of the repeated measures ANOVA did not reach statistical significance, $F(9, 380) = 1.75$, $p = 0.1199$. Given the non-significant findings, additional testing or a larger sample size may be necessary to determine the reliability of the observed trend. Modeling efforts to better understand this effect are currently underway (Freedland & Rieke, 2022).

3.4 Discussion

Motion on the Retina Dictates Performance on Acuity Tasks

As in previous investigations, we found that at short durations (3 frames), little benefit was derived from natural retinal motion compared to stabilized viewing. One reason for this may be that the eye has not had the time necessary to leverage the temporal component to seeing that is introduced with its movements, consistent with the results of computational studies on the role of FEM in spatial vision (Anderson et al., 2020; Burak et al., 2010). According to this view, without sufficient time, drift and tremor are unable to serve a useful purpose in improving performance on an acuity task, where temporal accumulation of dynamic retinal signals are key to deriving a benefit from FEM.

Crucially, we found that under the conditions studied in this chapter, no amount of retinal motion was beneficial for fine spatial vision. While our findings mirror previous work that suggests there is an upper limit to the velocity of drift and tremor motion that is optimal for visual acuity (Clark et al., 2022; Derrington et al., 2004), this must in balance with motion large enough to 1) reduce fading, 2) help resolve spatial frequencies near the resolution limit of the photoreceptor mosaic (Rossi & Roorda, 2010) and 3) whiten spatial frequency information (Rucci & Victor, 2015). Our investigation shows that a critical aspect of motion's consequences on fine spatial acuity depend not only on the magnitude, but also on the direction of motion. Most importantly, the interaction between a stimulus's features and the direction of motion is critical to performance outcomes.

While fixational eye movements that move in an orthogonal motion to a grating are helpful in seeing, if the velocity of sampling induces motion blur in particular motion directions, we found even at short durations similar FEM can shift from helpful to harmful. In our study, orthogonal motion to a stimulus's orientation proved to be the most difficult to resolve when the stimulus was moved so that the bars of the optotype alternated on a single patch of retina (Figure 3.4). Previous investigations have shown that allowing small fixational eye movements that are orthogonal to critical stimulus features improves acuity, and used a coarser spatial frequency and longer stimulus duration than the current investigation (Rucci et al., 2007). Showing alternating stimulus features, because of both the orthogonal motion and imposed motion of 1 bar width, was more deleterious to performance than an increase in total magnitude (Figure 3.4, imposed motion of 2).

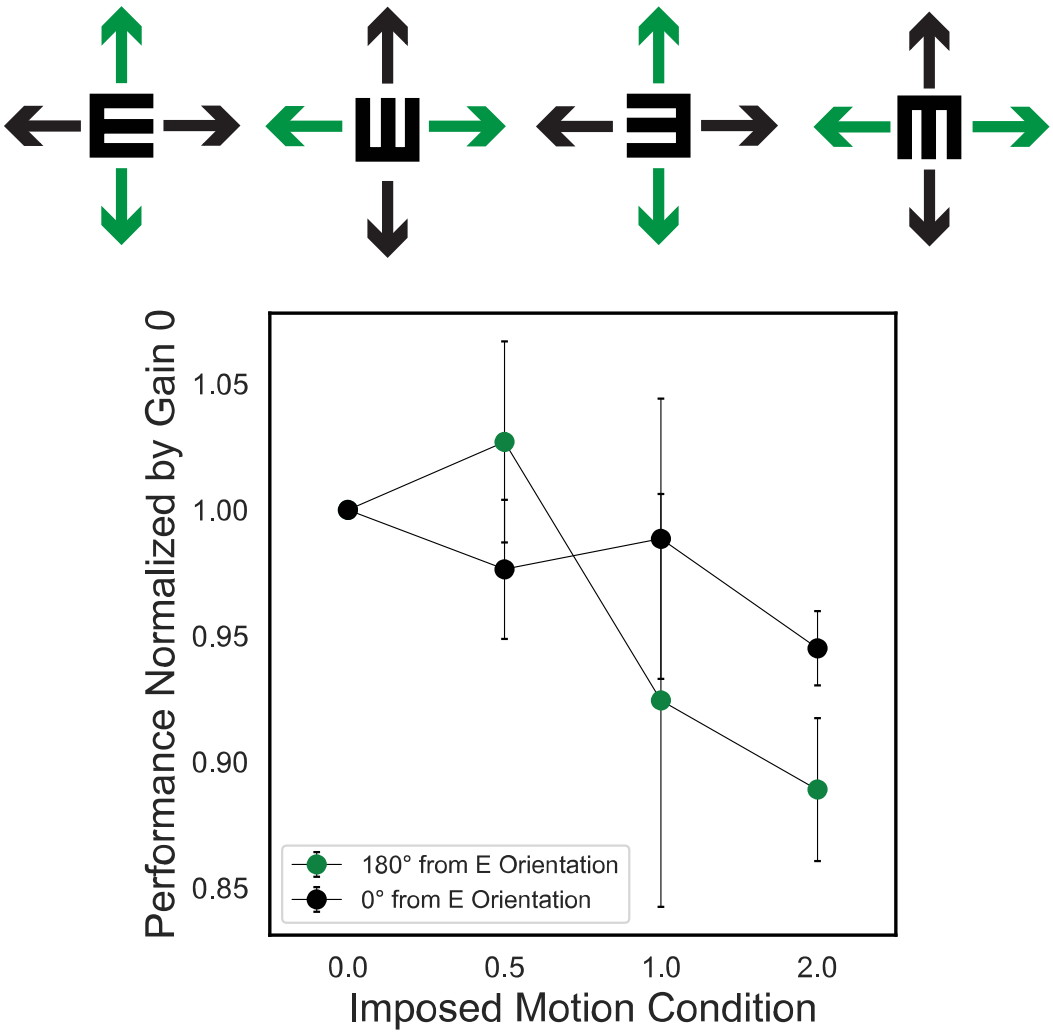


Figure 3.7: Stimuli were presented at 4 random cardinal directions, then moved in 1 of 4 random cardinal directions (top). In parallel trials, stimuli could move either 0 degrees from their orientation or in the opposite direction from its gap direction (180 degrees from orientation). Performance between these two trial types is shown here, normalized to individual subject performance on no imposed motion (gain 1) trials (bottom). Normalized performance of trials with different motion relative to the stimulus orientation with error bars ±1 SEM is shown.

Critically, this suggests that during the encoding stage of processing, the human visual system is limited in its ability to integrate short presentation, fine stimuli at the photoreceptor level (Cottaris et al., 2020). This integration limit could explain the motion blurring in these orthogonally moving stimuli we see in our results. It is therefore not only the magnitude of motion, but the direction of that motion which will determine if the features necessary for discrimination will be successfully resolved at fine spatial frequencies. We show this in stimulus presentations that are decoupled from individual differences in drift and tremor magnitude and direction. These findings prompt speculation on the implications for individuals with highly anisotropic drift tendencies. For instance, individuals prone to downward drift might display a more pronounced horizontal/vertical asymmetry in visual acuity measured under natural conditions, contrasting with those exhibiting more uniform drift patterns. Better understanding these individual differences could shed light on the nuanced relationship between drift tendencies and visual perception.

Underlying Outcomes that Influence Impaired Performance

It is critical to examine the types of errors that were made in our investigation in order to understand the underlying mechanisms influencing our main results. First, the difference in 90 and 180 degree errors shows that while subjects are generally able to resolve the vertical, most identifiable aspect of the stimulus (the vertical E bar), in the orthogonal imposed motion of 1 trials, there are effects from early vision that impact performance in only this motion direction (Figure 3.5). The increase of 90-degree errors is highly tuned to this one condition, suggesting that encoding errors as early as the photoreceptors may be the root cause of this indiscriminability.

While subjects generally guess evenly between all 4 cardinal directions regardless of the stimulus motion, when the optotype is not easily resolved, other strategies may be employed when one is forced to respond. Because the orthogonally moving stimulus at an imposed motion of 1 bar width is more difficult to resolve, the visual system may rely on other cues to inform its perception about what the stimulus orientation is based on the task demands (Figure 3.6). This cue combination optimization of orientation with motion is not unlike findings in other cross-cue work (Ernst & Banks, 2002). If one cue is uncertain, a different, more salient cue type may be substituted to inform an overall percept.

These error types can more generally be explained by motion blurring – where the relationship of stimulus motion to the bars of the E (see Figure 3.2) could be detrimental in the imposed motion of 1 bar orthogonal, but not parallel, trials. Clearly, the same patches of retina becoming exposed to opposing (dark-light-dark or vice versa) stimulus features would cause deficiencies in those photoreceptors' ability to clearly resolve the stimulus. Thus, predetermined, highly controlled imposed motion conditions give insight into how the effects of motion blur may be detrimental to fine spatial vision at short durations.

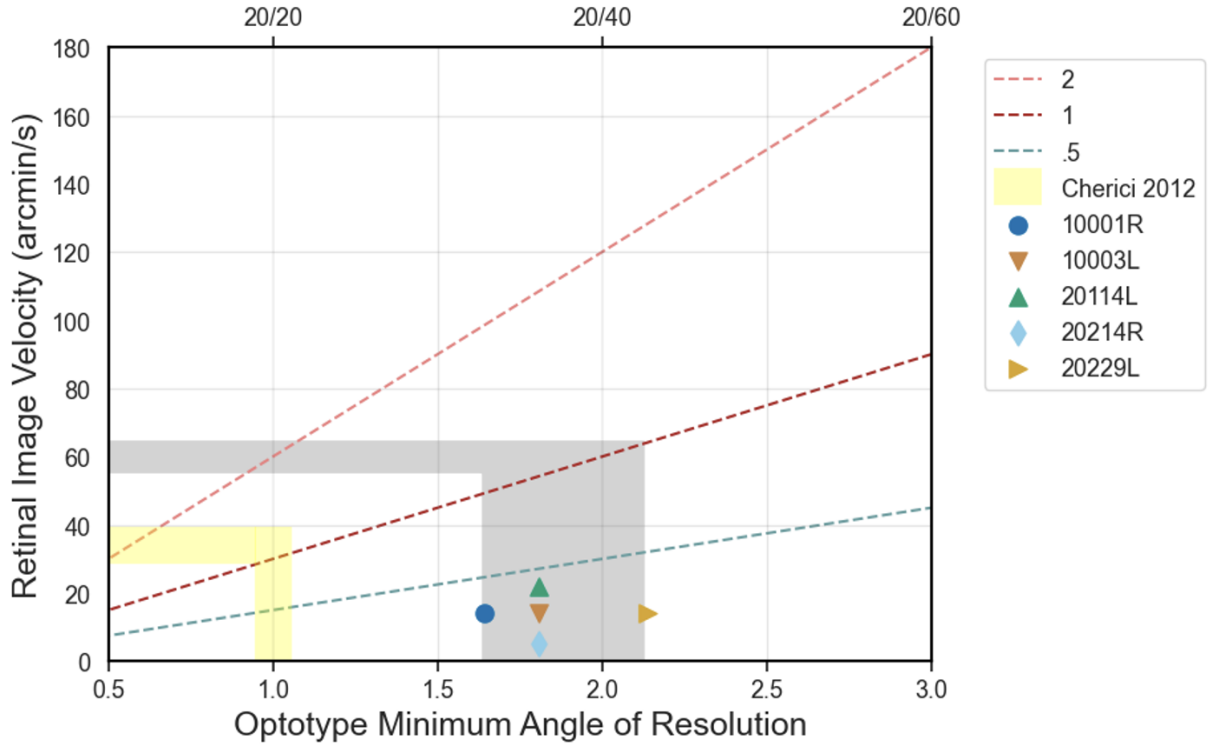


Figure 3.8: The velocity at which the stimulus moves on the retina during the 0.5, 1 and 2 motion conditions varies with optotype size (in minimum angle of resolution) because the frame by frame difference is relative to the bar width. Each subject performed a staircase procedure to assign a letter size that led to consistent performance in unstabilized viewing (80%). Crucially, there are then differences in velocity during the experiment by individual, dictated by the size of the stimulus. The velocity increases linearly as MAR increases across each imposed motion condition. The larger imposed motion values lead to relatively larger increases in velocity compared to smaller imposed motion values.

Comparison to Natural FEM

Our study purposefully employs an instantaneous velocity higher than natural ocular drift because we present stimuli at 1 degree temporally from the preferred retinal locus to avoid any effects of chasing (Wu & Cavanagh, 2016). An equivalent stimulus necessary to achieve 80% performance on a visual acuity task at the fovea would likely be near ∼35 arcmin/second, or the velocity used in this investigation (Cherici et al., 2012). Figure 3.8 confirms this conclusion. In other words, this type of motion on the photoreceptor mosaic could reasonably be produced by natural drift. Our motion imposed retinal image velocities are similar to what might be expected from natural drift motion.

3.5 Conclusion

In conclusion, a recent renewed interest in fixational eye movements has significantly contributed to our understanding of visual processing mechanisms, particularly in relation to perception with and without drift and tremor's impact on fine spatial acuity. This investigation supports the notion that there are fundamental limits imposed by individual photoreceptors to the human visual system. By precisely controlling the time course and trajectory of stimuli on the retina, we can categorize the point at which retinal motion goes from beneficial to harmful to fine spatial acuity. It is crucial to acknowledge that not all types of motion are equal, as fundamental limits exist in the encoding of temporal information during early stages of visual processing. These limits are based on the amount of photoreceptor sampling that might occur over a stimulus presentation, which depend on the features of a stimulus being shown.

While retinal motion can be helpful in resolving fine spatial stimuli, post receptoral visual processing areas are unable to interpret a stimulus that is blurred by motion at the beginning stages of vision. Thus, visual acuity is limited not only to optical and neural factors, but also physiological variables such as the temporal integration window of a single photoreceptor. These findings help categorize the conditions under which motion is helpful and harmful to acuity and show that these conditions are dependent on the stimulus. While motion can be beneficial to spatial vision, not all motion is equally as useful in aiding acuity.

Chapter 4

Contrast Sensitivity in Stabilized and Naturally Viewed Stimuli at the Parafoveal Retina

4.1 Introduction

There has been much interest in the field of vision science on the purpose of fixational eye movements. The smallest movements of the eye, drift and tremor, have many effects on perception (Boi et al., 2017; Rucci & Victor, 2015). While it is clear that eliminating this motion is harmful to acuity, the full extent of their usefulness has yet to be understood (Ratnam et al., 2017). Even though drift and tremor motion is clearly important for visual perception, it has been suggested that the eye's natural movements are not optimal (Ağaoğlu et al., 2018). While there have been efforts to study the effects of removing FEM on performance tasks, this has never been tested on a contrast sensitivity function (CSF) obtained under gaze-contingent, AO-corrected conditions. The contrast sensitivity function models the response threshold of luminance variations. Typically, this is done by psychophysically testing the lowest detectable luminance change in gratings across various spatial frequencies (Campbell & Robson, 1968; Robson, 1966). The highest spatial frequencies are thought to be limited by optical factors, while the lower end is limited by neural factors (Breitmeyer & Julesz, 1975; Robson, 1966). Many stimulus characteristics influence the ability to discriminate gratings, including stimulus onset (Breitmeyer & Julesz, 1975), duration (Watt, 1987), eccentricity and meridian (Abrams et al., 2012; Himmelberg et al., 2020). By testing the CSF with and without eye motion, we can better understand the beneficial role FEM play on various spatial frequencies.

By using an adaptive optics scanning laser ophthalmoscope (AOSLO), we can test the effects of FEM on the finest perceptible spatial frequencies in the human eye. The AOSLO removes almost all limitations imposed by optical factors of the visual system (Roorda et al., 2002). This leaves only stimulus features, photoreceptor packing, eye movements and pho-

toreceptoral processing as variables that influence acuity. Previous studies have attempted to categorize the relationship between spatio-temporal processing of gratings (Watson & Nachmias, 1977). However, these relied on dated cathode ray tube displays, where factors such as eye movements may have confounded results. Using the latest eye tracking and stimulus display technology, we can isolate the effects of our findings to only a few factors, and thus better understand the usefulness of motion in visual processing.

Many studies have shown that fixational eye movements have the largest impact on fine stimuli (Rucci et al., 2007). First, retinal motion is thought to help sample an otherwise under sampled stimulus (Anderson et al., 2020). The motion of the retina is thought to add a temporal component to vision that can be used to decode a stimulus that is fine enough that photoreceptors might not be able to clearly resolve it. Second, fixational eye movements are thought to whiten fine stimuli, amplifying the photoreceptor response to fine spatial frequencies (Boi et al., 2017; Rucci & Victor, 2015). While effects of medium (10 cycles per degree, CPD) and low (1 CPD) spatial frequency gratings have been tested with and without the effects of FEM (Rucci et al., 2018), a major gap in the existing literature is that the contrast sensitivity function has never been measured with and without the eye's most fine movements while controlling for optical aberrations. This study aims to fill this gap, as well as offer new insights into the mechanisms that underlie the effects of fixational eye movements. This chapter outlines a detailed overview of an investigation that will help answer some of the remaining fundamental questions of how fixational movements help and hurt the perception of fine spatial detail. All results are hypothetical, but draw from the existing literature to propose expected results and interpretations of the anticipated findings.

4.2 Methods

Participants

5 subjects with no known retinal disease will be recruited for the study. Informed consent will be granted from each subject and all procedures will adhere to the Declaration of Helsinki.

Apparatus & Stimuli

An adaptive optics scanning laser ophthalmoscope will be used for both stimulus presentation and data collection (Roorda et al., 2002; Wang et al., 2019). All subjects will be dilated with 1% Tropicamide approximately 15 minutes before the experiment. Subjects will create a custom molded bite bar to keep their head immobilized during the experiment.

Detailed technical specifications have been outlined in Chapters 2 and 3. In short, infrared light will be used for imaging (wavelength: 840 ± 25 nm; luminance: yet to be measured) and wavefront sensing (wavelength: 940 nm) will be achieved using a supercontinuum laser source (SuperK Extreme; NKT Photonics, Birkerød, Denmark). Higher order aberrations will be corrected using wavefront sensing and correcting technology (Shack-Hartmann wavefront

sensor, DM97-08; ALPAO, Montbonnot-Saint-Martin, France). The vertical and horizontal scanning nature of the system will create the percept of a dim red square. Image light reflected from the retina will be digitized to produce a 512 × 512 pixel retinal image at 30 frames per second. The square raster will subtend an optimal field for eye movement tracking and stabilization, yet to be determined.

For each stimulus presentation, the laser will be modulated to produce a negative contrast 2-AFC tilted grating. While these gratings are typically sinusoidal (Robson, 1966), here we will use square gratings, which may improve sensitivity (Breitmeyer & Julesz, 1975). The contrast of the grating will be adjusted by manipulating the intensity of the laser for each trial.

The grating will ultimately be displayed for a fraction of the 30 Hz frame, and thus the total duration will be dependent on stimulus size (see Figure 4.1). Duration is not a focus of this experiment, so we will describe the stimulus presentation in frames to stay true to the technical specifications of the AOSLO. Subjects will be instructed to report the orientation (left or right) of the grating using a gamepad. We will use a method of constant stimuli for various spatial frequencies and contrasts to find thresholds of orientation discrimination between retinal image motion conditions.

The AOSLO system can track the movement of the photoreceptor mosaic and move the stimulus within the raster field to remove the effects of FEM motion using custom built software (Stevenson et al., 2010). All measurements will be taken at 1 degree temporally from the foveal center to avoid chasing behavior induced by stabilization. As in Chapters 2 & 3, trials where the stimulus moves in the world in order to stay on the same patch of cones during a trial are called 'stabilized' or have a gain of 1 relative to drift and tremor. Stimuli that stay in world fixed coordinates are 'unstabilized' or gain 0.

Experimental Procedure

We will use an orientation discrimination task to examine the effects of retinal stabilization on fine spatial vision. Broadly, we will measure the CSF across different motion conditions for each subject at various spatial frequencies between our low and high benchmarks. Each stimulus will be shown for 4 frames in the AOSLO. Similar to previous studies, we will assess visual performance using a stimulus whose spatial properties remain fixed across subjects rather than adjusting its size to measure an acuity threshold (Ratnam et al., 2017; Rucci et al., 2007). So, for each subject, a fixed sampling spatial frequency (between 60 and 1 CPD) will be displayed while contrast will be manipulated. Trials will be randomly interleaved between stabilized and unstabilized and randomly sampled from spatial frequency and contrast levels. This will then be fit with a psychometric function and threshold will be reported at 75% (halfway between chance and ceiling performance).

We will test visual acuity at the limit of the human photoreceptor limit at one degree of eccentricity. The finest (60 CPD) stimulus should probe acuity at the Nyquist limit of human vision at this eccentricity (Rossi & Roorda, 2009). Stimuli should then evenly sample a range of spatial frequencies. 11 CPD should be included in stimulus spatial frequencies

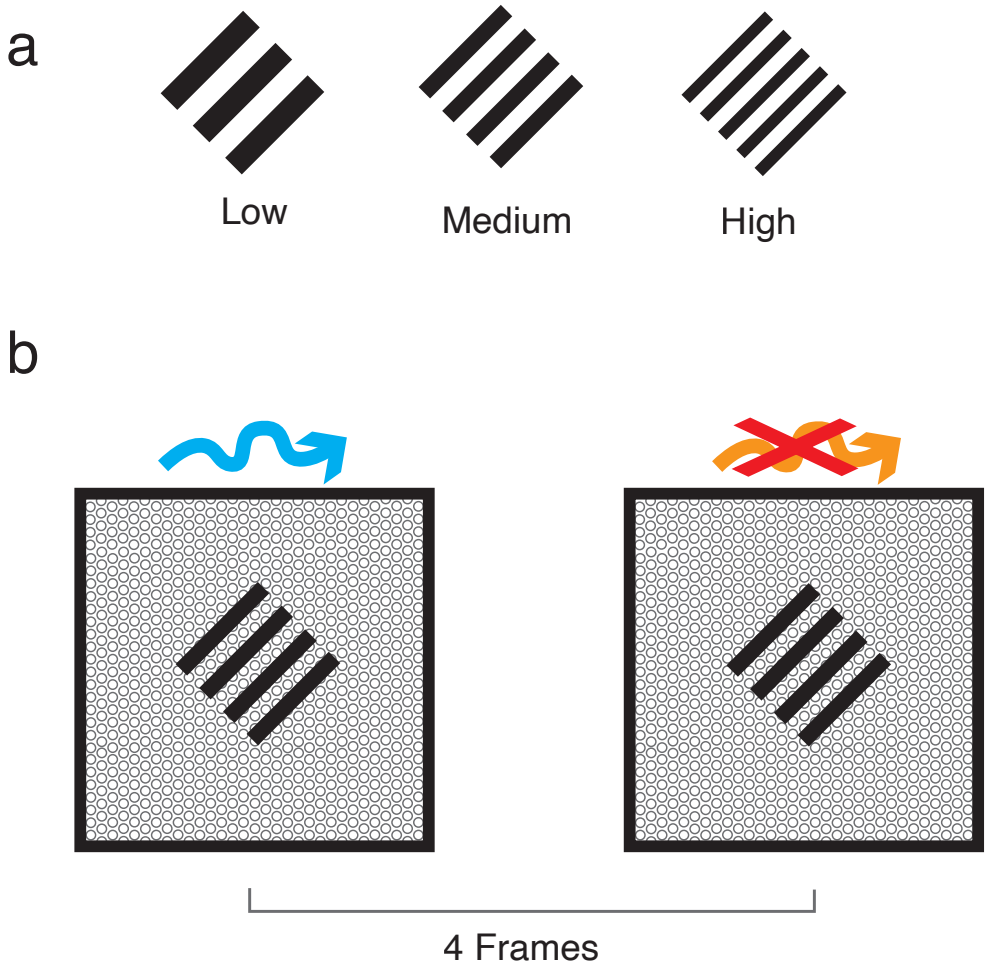


Figure 4.1: a. Various gratings (60 to 1 CPD) ranging from very high to low spatial frequencies will be shown to subjects in a 2-AFC orientation task while varying contrast via laser intensity. b. These will be either unstabilized or stabilized on the retina for 4 frames in the AO system.

(Rucci et al., 2007) to compare our findings to previous results. The most coarse stimulus should test the limits of neural factors at 1 CPD. The number of spatial frequencies will be up to the discretion of the research team's bandwidth for running subjects. Ideally, between 6 to 8 spatial frequencies will be tested (Chung & Legge, 2016). For the purposes of this dissertation, we will use the labels 'high CPD', 'medium CPD' and 'low CPD' to show our expected results.

Eye Movement Analysis

Trials should be removed based on several criteria. All types of trials should be excluded if microsaccades occurred during stimulus presentation (Clark et al., 2022; Ratnam et al., 2017). In addition, stimuli that were not properly stabilized on the retina should be removed (see Chapter 2 for detailed description). Briefly, this should utilize a move-means (as opposed to a k-means, as in Chapter 2) approach where the image data should match a template with 90% correlation for 90% of the frames.

Second, stimuli that did not travel the expected amplitude and direction during the imposed motion condition should be removed. The videos should then be reviewed and excluded by hand to ensure accuracy.

4.3 Hypothetical Results

Hypothetical results are outlined below. The difference in the contrast sensitivity function between stabilized and natural motion is shown in Figure 4.2. Contrast sensitivity is expected to be lower overall in all stabilized stimulus (Ratnam et al., 2017), with a shift away from higher CPD due to loss of reformatting (Boi et al., 2017; Rucci et al., 2007). This will present as a shift leftwards (Intoy & Rucci, 2020), as drift is thought to amplify the perception of high spatial frequency stimuli.

In sum, we expect that stabilization will change the CSF for different spatial frequencies under different motion conditions. We expect that stabilization will deleteriously impact the CSF across all spatial frequencies. The CSF should also shift to the left as a result of removing drift and tremor, which are thought to aid in perception of the highest spatial frequencies.

4.4 Discussion of Expected Results

These results should help answer the question of how retinal image motion changes visual perception of stimuli at the finest resolvable spatial frequencies.

Comparing the contrast sensitivity functions of the stabilized compared to natural motion conditions will help gain further insight into the mechanisms behind why retinal motion is beneficial to fine spatial acuity. Shifts in the CSF curve would suggest that the limitations

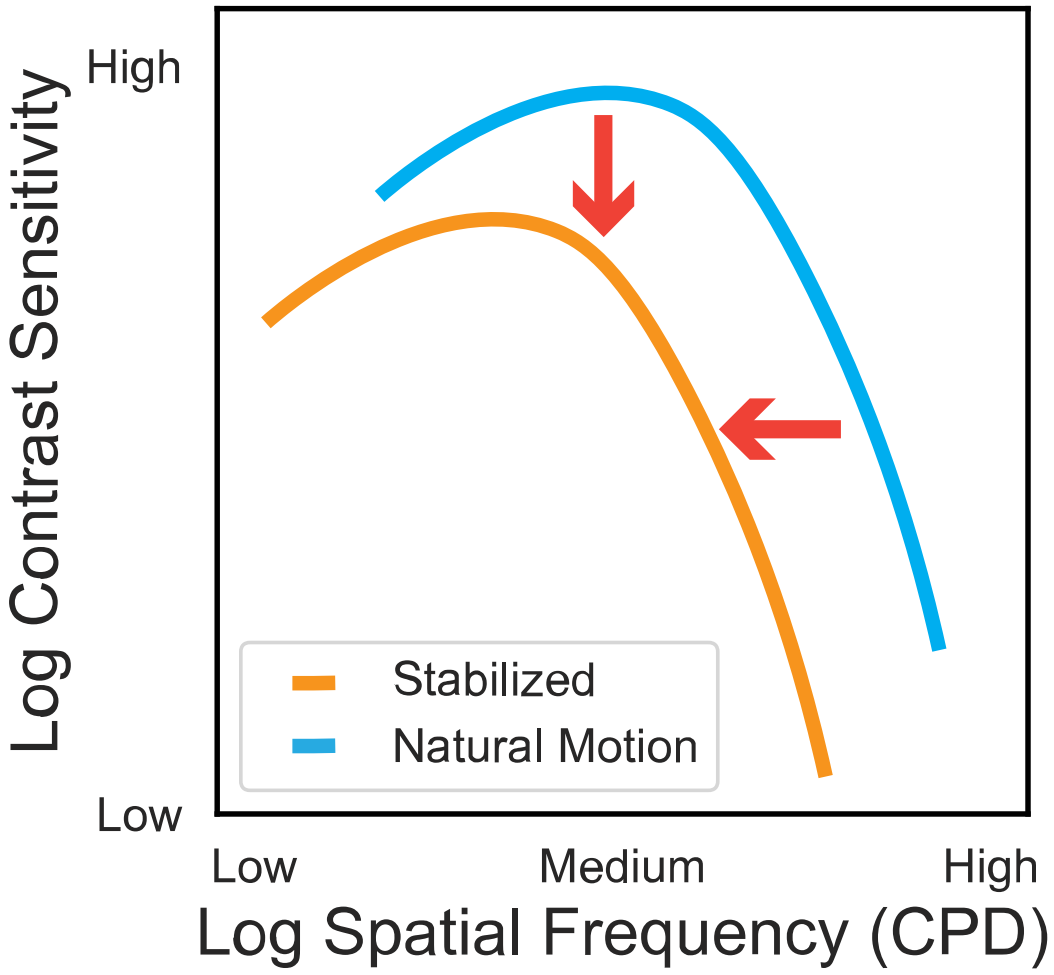


Figure 4.2: Stabilized and unstabilized CSF are averaged across subjects. Shifts in the CSF are highlighted by red arrows.

imposed by stabilization are rooted in changes in contrast. This has been suggested by a number of studies (Rucci et al., 2007), but never fully tested in humans.

A growing body of literature suggests that motion on the retina will be more beneficial to acuity for finer stimulus spatial frequencies. There have been suggestions that eye movements help to whiten fine spatial frequency stimuli (Boi et al., 2017). This computational work has been proven psychophysically in more coarse stimuli (Rucci et al., 2007), and while we expect the results to hold constant for finer spatial frequencies, a thorough test of the CSF with single-photoreceptor level control of stimulus position is essential to answering this question.

In conclusion, the experiment outlined here should help catalog the impacts of fixational eye movements on acuity. By measuring contrast sensitivity, we can further explore the underlying mechanisms of why stabilizing a stimulus hurts the ability to see fine detail. This should lead to a more comprehensive understanding of why the eye is never fully at rest.

Chapter 5

General Discussion

The usefulness of fixational eye movements have long been debated in the field of vision science. Only more recently have they been recognized as crucial elements in human visual perception. The dominant line of research has focused solely on their usefulness in improving acuity - reformatting high spatial frequency information and adding a temporal element helpful in decoding visual stimuli. However, there should theoretically be drawbacks to introducing motion. This dissertation examined how there are limitations to the usefulness of movements which are temporally dependent. We also described the various components of potential disadvantages of dynamic vision, as we found that not all motion is beneficial to vision.

In Chapter 2, I present findings that suggest FEM are only beneficial to the visual system's ability to resolve fine spatial information if the stimulus duration exceeds a certain threshold. The eye and brain require sufficient time to move and sample the visual scene effectively. Beyond a certain minimum duration, the removal of FEM negatively impacts acuity. This suggests that there is a balance in FEM's utility that is temporally dependent. At certain timepoints, enough benefit is accrued from motion that removing FEM hurts performance. At short stimulus durations, this is no longer the case. We show that there is a tipping point to stimulus duration, after which FEM become useful.

The findings of Chapter 3 suggest that contrary to the field's popular belief, not all FEM motion is beneficial to acuity. By moving stimuli either parallel or orthogonal to a stimulus's critical elements, features needed to properly resolve a stimulus were more or less blurred. This is independent of individual FEM tendencies. I show how motion direction can be more detrimental to acuity than introducing a larger magnitude. The extent of motion blur is contingent upon the features of the stimulus being observed, underscoring the complex interplay between FEM and visual stimuli.

Chapter 4 outlines the methods and results for an experiment which would help to solidify the idea that fixational eye movements change vision depending on the spatial frequency of visual inputs. By using modern methods to measure the contrast sensitivity function in relationship to natural and stabilized motion conditions, we can put real human psychophysical data to the concepts that have been proposed by many in the field. We expect these

findings to help answer decades long questions about what FEM do to change spatial vision across stimulus types.

In sum, this dissertation contributes valuable insights into the effects of fixational eye movements on human visual perception. It underscores the temporal and motion-related dynamics that influence the utility of FEM. By probing the complexities of FEM and their effects on recoding visual perception, this research sets the stage for future investigations aimed at enhancing our understanding of the basic underlying mechanisms of human vision. Ultimately, we have used psychophysics and laser ophthalmology to explore the interactions between physiology and cognitive neuroscience to better understand the complexities of human vision.

Chapter 6

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Appendix A

Supplemental Materials for Chapter 2

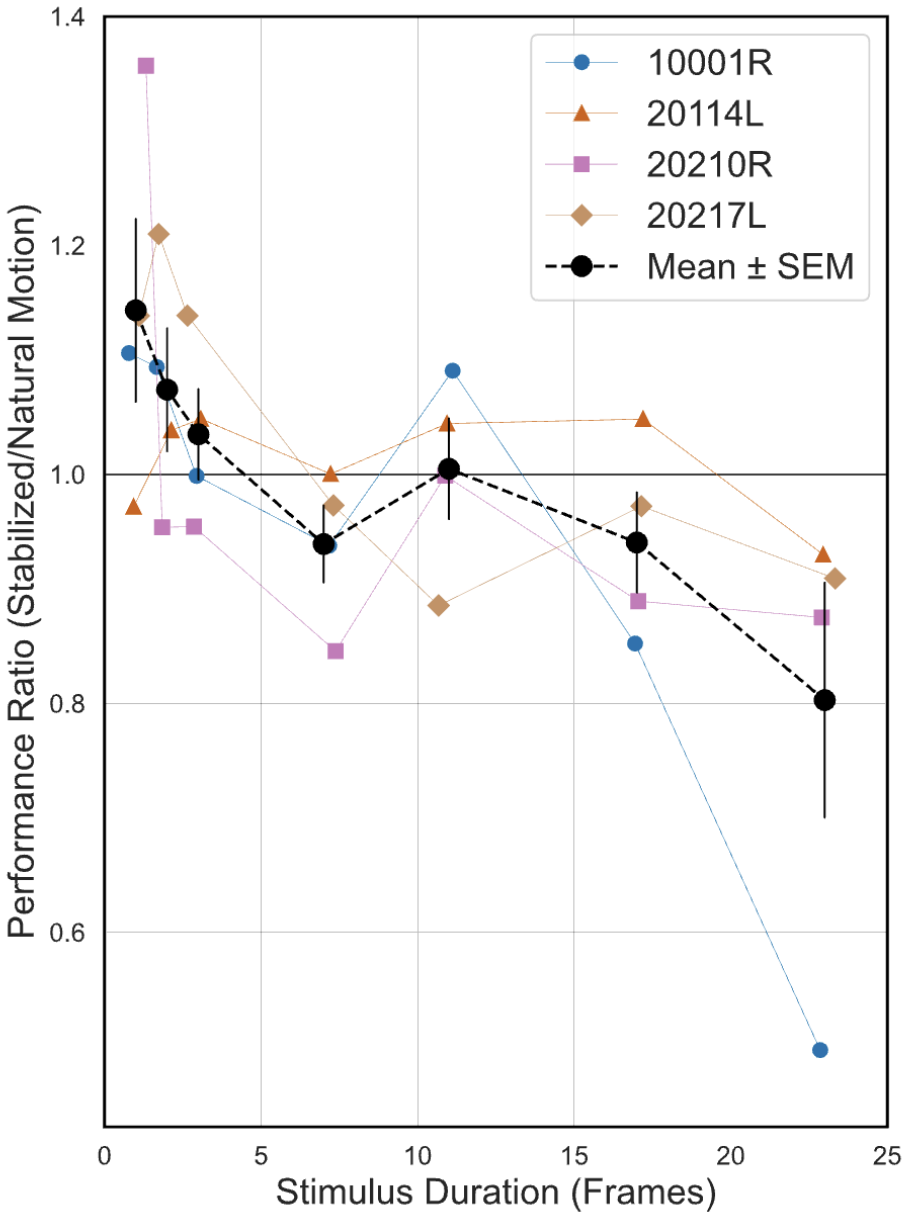

Figure A.1: Performance ratios from the blocked data collection protocol. Specifically, this protocol was to show subjects 100 stabilized and 100 unstabilized trials across various durations.

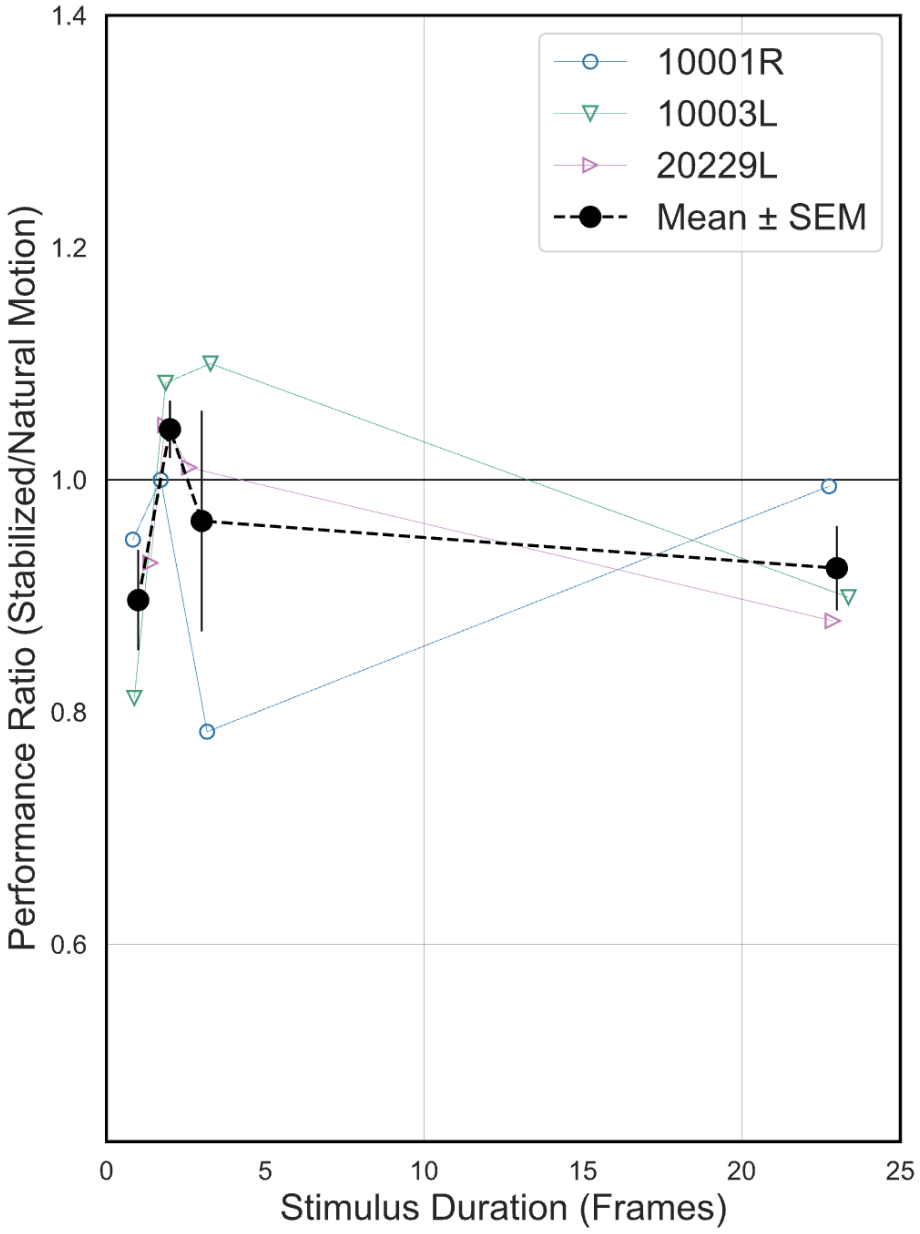

Figure A.2: Interleaved design performance ratio. This protocol randomly interleaved stabilized and unstabilized trials in a 100-trial block across 4 durations.

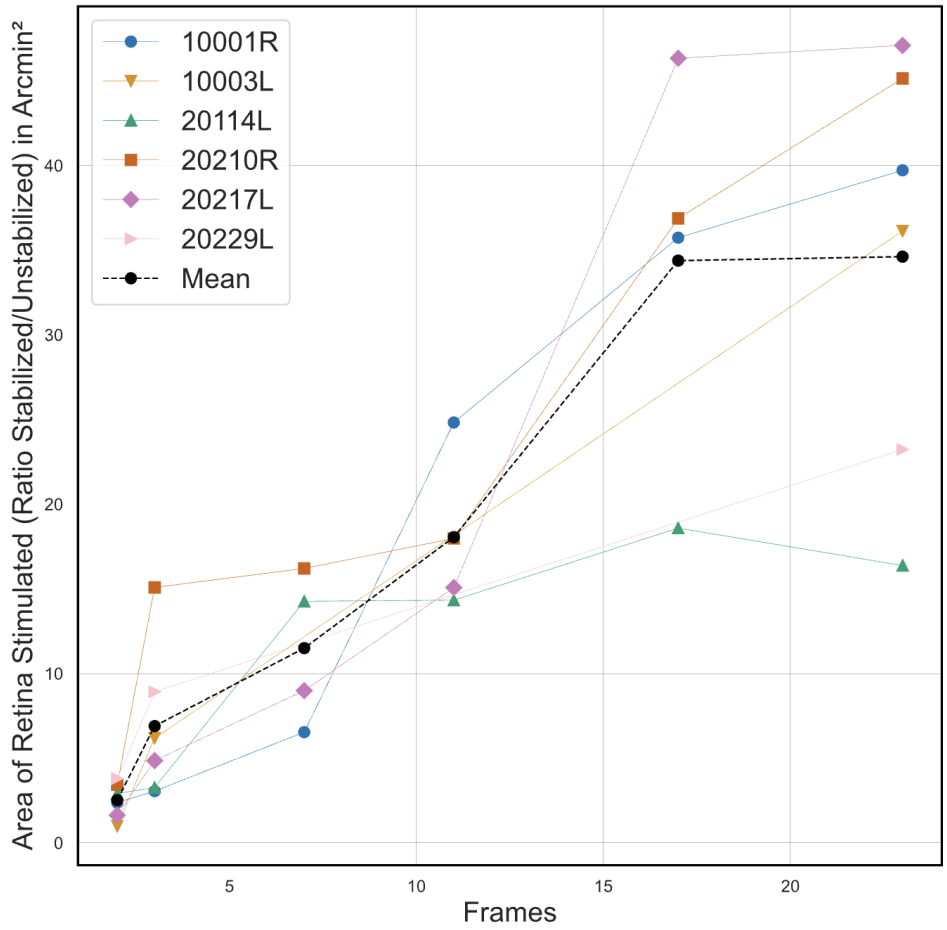

Figure A.3: Ratio (stabilized/unstabilized) of area of the retina that was stimulated (ISOA contour of 68%) across all frames, in arcmin^2.

Appendix B

Supplemental Materials for Chapter 3

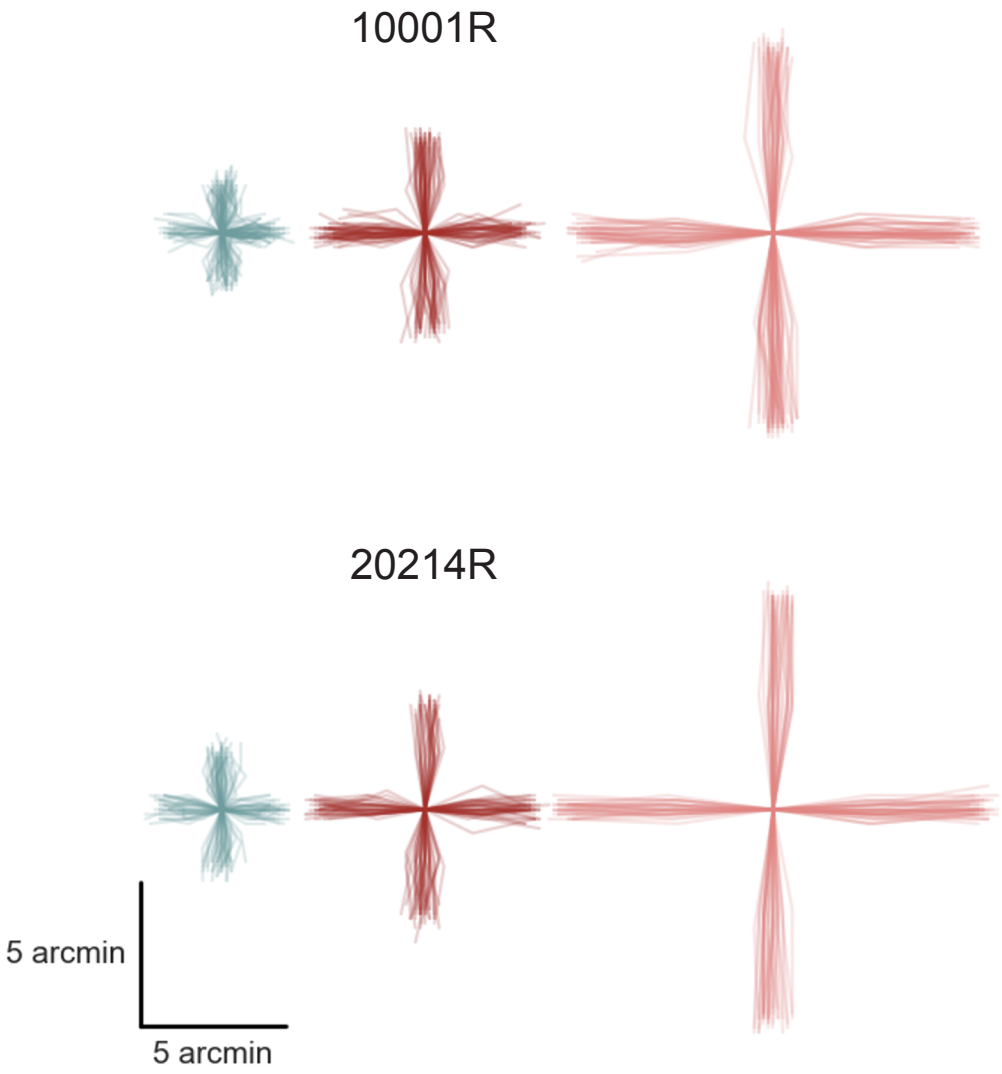

Figure B.1: Exact stimulus trajectories on the retina were extracted from the locations of the E on the retina for 3 frames. Using these locations, we can verify the velocity of the imposed motion condition for each trial. Here, we show imposed motion for each condition ranging from 0.5, 1 and 2 bar widths per frame (over three frames) for two subjects. As shown in the figures, the sampling of the retina increased with an increase in the imposed motion factor across subjects. These traces include variations seen from the eye's natural movements over 3 frames (∼100 ms).