INDIVIDUAL DIFFERENCES IN SLOW-MOTION THRESHOLDS

by

JACOB BRANTLEY HARTH

(Under the Direction of Lisa M. Renzi-Hammond)

ABSTRACT

Despite perception being generally perceived as a coherent whole, the underlying physiology is primarily a process of deconstruction followed by reconstruction. Processing a visual image, for instance, requires decomposition into its component parts such as color, depth, and form. These features are then relayed down relatively independent pathways that are then analyzed in discrete cortical regions (e.g., V4 for color) to later be recombined into a meaningful perceptual whole. Global motion processing is no exception. Most descriptive models describe motion processing as a relatively binomial process, one that mediates slow motion and the other that processes fast motion. Although the fast-motion system has been well studied (including its various drivers/covariates), the slow-motion system has been less well characterized. In this study, we designed a system to measure slow-motion thresholds in a sample of young, healthy adults. The results showed substantial variability across individuals (on average ranging by a factor of approximately 38 across participants with similar age, sex, refractive state, etc.). Lutein and zeaxanthin status was not related to the slow-motion system despite being known to drive individual differences in the fast-motion system.

INDEX WORDS: Motion perception, Slow motion, Lutein, Zeaxanthin, Macular pigment

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DEDICATION

To my parents, who inspired in me a love for learning.

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CHAPTER 1

INTRODUCTION

Motion perception is a fundamental visual process that involves seeing a stimulus move through space and time. It is easy to take this ability for granted in daily life or to not fully consider its essential nature. The ability to sense and perceive motion, however, is crucial for the construction of a normal visual experience. The importance of acute central and peripheral vision, especially in the context of movement, is paramount for normal function and safety. From an ethological perspective, the ability to accurately detect motion at its most liminal point provides a distinct survival advantage. Seeing motion in the modern world is vital to complex visuomotor activities (e.g., driving and athletics) and for activities of daily living such as household chores and spatial navigation during locomotion.

Seeing a stimulus move, in essence, depends on the sequential activation of photoreceptors that results from a serial change in a visual stimulus. Schouten (1967), for example, argued that a neural model of motion perception can be quite simple: essentially two neurons separated by a fixed distance that feed into a movement detector. This movement detector will only respond if the first receptor is activated and then the second is activated within a given amount of time (i.e., directional and temporal tuning). As with most processes in vision, the ultimate perception of motion is nonetheless complex and multi-level (see Nishida et al., 2018 for a thorough review). For example, in a real-world setting (i.e., when the eye is not stabilized), the source of image movement on the retina must be discriminated from eye and head movements. Gregory (1977) originally postulated the presence of at least two interdependent

systems: the image-retina and the eye-head systems. The image-retina system is essentially based on a moving external stimulus that produces successive stimulation of adjacent retinal loci. This sort of movement detection is well-suited to the mosaic of ommatidia in the compound eye of arthropods (e.g., *Limulus polyphemus*), and these simple systems are used to study this type of primitive motion detection (Gregory, 2015). The eye-head system incorporates visual, vestibular, and proprioceptive information from the movement of the eyes, the head, and the body to contextualize and perceive movement when the retinal image may be misleading (e.g., when the eyes track a moving object). In the present study, we investigated the image-retina model of motion perception.

Motion perception has been extensively investigated and characterized in many ways (Nakayama, 1985; Burr & Thompson, 2011), with entire fields of study focusing on specific types of motion (e.g., biological motion perception) or motion in context (e.g., speed perception). The use of different stimuli in motion perception investigations has contributed in part to variable conclusions about the mechanisms underlying motion processing. Random dot stimuli and sinusoidal gratings, for instance, have been used to measure signal-to-noise ratios and the influence of sensitivity to spatial and temporal frequencies (Cavanagh et al., 1985). Depending on the stimulus, context, and observer, there could be endless investigations into different aspects of motion perception. In the present investigation, we simply measured the slowest motion an individual had the capacity to detect.

Two Motion Systems: Fast and Slow

A common framework for understanding global motion perception posits that there are at least two relatively independent systems involved: one system mediates motion at the minimum (i.e., the slowest speeds) and the other at the maximum (i.e., the fastest speeds). This framing

(e.g., Gorea et al., 1993a; Gorea et al., 1993b; Holcombe, 2009) resembles spatial vision where low and high spatial frequencies are thought to be relayed by independent channels and processed in parallel (Sachs et al., 1971). The slow-motion system detects change at the lowest threshold of movement (the slowest stimulus we can perceive), whereas the other determines the upper limiting range (the fastest motion we can detect). This type of division of visual information processing into functionally complementary pathways is a common feature of the visual system (magnocellular and parvocellular pathways, dorsal and ventral streams, etc.). The neurophysiological underpinnings of these systems have been carefully determined. This is also true of the fast- and slow-motion systems.

Motion as a Multi-Level Process

The overall processing of motion is thought to reflect a collection of neuronal mechanisms, each with different sensitivity, that are pooled together to create a cohesive percept. In many areas of visual perception research, the number and nature of these mechanisms (i.e., channels) have long been debated. For example, some argue that the contrast sensitivity function is mediated by multiple discrete spatial frequency channels, while others argue for only two channels (two seems to be the emerging consensus; Reynaud & Hess, 2017). The visual system must deconstruct disparate elements of a scene (e.g., motion, color, spatial content) and then reconstruct them to create an internal percept (based loosely on external reality) that leads to predictable responses. The saliency of this challenge is demonstrated when one must respond to moving stimuli which often require an adaptive response (e.g., avoiding a flying object). The underlying neural physiology involved in creating this highly efficient and predictable system has been widely studied.

Like contrast sensitivity, global motion appears to be processed in parallel by two relatively discrete systems: a specific system for fast motion that selectively processes color and luminance and independently extracts motion signals before combining them and an unspecific system for slow motion that combines color and luminance information prior to the extraction of motion signals (Gorea et al., 1993a; Gorea et al., 1993b). Psychophysical data on motion afterimages is also consistent with this functional division of the fast-motion system and the slow-motion system. Random-dot stimuli with both fast-moving and slow-moving targets produce the simultaneous presence of both dynamic and static motion afterimages (Van Der Smagt et al., 1999). This functional independence is well explained by physiologically distinct processing of fast-motion and slow-motion information (i.e., occurs at different levels of the nervous system).

The neurophysiological basis of these systems has been investigated in primates and humans. Primate studies in the macaque visual cortex reveal selective responsivity of Brodmann area 17 (i.e., extrastriate area V1) to slow motion and selective responsivity of middle temporal area (MT) (i.e., extrastriate area V5) to fast motion (Mikami et al., 1986; Newsome et al., 1986). Lappin and colleagues (2009), based on psychophysical studies on humans, investigated the effects of speed, eccentricity, and low vision on the spatiotemporal thresholds of motion perception; they concluded that spatial resolution limits the lower thresholds for slow-motion detection whereas temporal resolution likely determines the upper thresholds for fast-motion detection. Slow-motion perception is primarily governed by retinal physiology (e.g., lateral inhibition) and therefore more affected by optical factors (e.g., temporal chromatic aberrations, Mullen et al., 2003). Fast-motion perception is likely primarily processed cortically, or further downstream in the visual system, as demonstrated by its strong relation to flicker perception

(Holcombe, 2009) and by blood oxygen level dependent (BOLD) responses to fast motion in the visual cortex (Mikellidou et al., 2018). An individual's threshold for visual temporal processing, or how "fast" they can see, is determined post-receptorally by cortical mechanisms (Skottun, 2013). The relation between the upper limits of temporal processing speed (e.g., critical flicker fusion threshold, CFF) and the perception of fast motion indicates likely concomitant processing.

Clinical evidence in humans is a good demonstration of the multi-level nature of motion perception[1]. Case studies have shown that when individuals sustain bilateral damage to the upper occipital gyri and adjacent MT gyri, they lose the ability to perceive motion faster than 10-deg/second but maintain normal perception (i.e., same as control group) of stimuli moving at 9-deg/second and slower (Zihl et al., 1983; Zihl et al., 1991; Heutink et al., 2019). In contrast, individuals with extensive lesions to area V1 have been shown to be consciously aware of the nature and direction of fast-moving stimuli, but this ability disappeared as speeds slowed, approaching 5-deg/second (Barbur et al., 1993). These case studies further demonstrate that fast and slow motion are processed by physically discrete pathways and brain regions and highlight an important distinction: slow-motion thresholds are determined early in the visual system (front end) whereas fast-motion thresholds are post-receptoral (i.e., the brain is the rate limiting step).

Individual Differences in Motion Perception

Wide individual differences in the ability to see motion, both at its lowest and highest range (slow and fast), have been noted in the literature for over a century (Exner, 1888; Brown, 1931; Crook, 1937). This range, even in young, healthy individuals, is dramatic (i.e., a factor of ten in some samples; Pilz et al., 2017). A large body of data also suggests that these differences

[1] Many seemingly coherent features of sensory systems are best understood as multi-level. For example, color is first processed by three cone types within the retina and then later processed by opponent cells post-receptorally. Sound waves are initially segregated via physical characteristics of the basilar membrane, but the perception of pitch is post-basilar (e.g., tonotopic organization of the auditory cortex).

are meaningful. At the extremes, they can indicate neurological issues. Deficits in global motion sensitivity, for example, often indicate neurodevelopmental disorders (e.g., dorsal-stream vulnerability; Braddick et al., 2003). Optimal motion detection in normal adults, however, appears to be driven by visual experience or training (Seitz et al., 2006) and health behaviors. As an example of the latter, the neuropigments lutein and zeaxanthin appear to be significant.

The Effect of Lutein and Zeaxanthin on the Fast-Motion System

The dietary xanthophylls lutein (L) and zeaxanthin (Z) are yellow/orange plant pigments found in leafy greens and other colorful fruits and vegetables. L+Z act as effective antioxidants and shortwave light filters (with peak absorption at around 460-nm). When primates consume sufficient concentrations of L+Z, these xanthophylls can cross the blood retina barrier and selectively accumulate in the macular region of the central retina, while also accumulating in the brain (Vishwanathan et al., 2013). When found in the retina, L+Z along with isomer meso-zeaxanthin are together termed macular pigment (MP). An exponential decay function best describes the spatial distribution of MP in the human retina, meaning that the highest concentrations of MP are present in the central 3-degrees, whereas minimal optically measurable MP is present beyond the central 7-degrees (Wooten & Hammond, 2005). L+Z levels measured in the human retina correlate with levels present in the occipital cortex and other brain regions (Vishwanathan et al., 2016); this indicates that measurement of MP optical density (MPOD) by a non-invasive psychophysical technique (e.g., customized heterochromatic flicker photometry) can provide information about cortical L+Z status. Humans cannot endogenously produce these xanthophylls, so they must be obtained through dietary intake. L+Z optimizes the development, function, and longevity of healthy human brains and visual systems (Stringham & Hammond, 2005; Hammond, 2008; Stringham et al., 2010; Johnson, 2014), emphasizing the need to

encourage adequate L+Z levels through dietary intake of fruits and vegetables (Krinsky & Johnson, 2005).

The substantial role of L+Z in promoting and preserving eye health, especially among older adults, is well established (see Krinsky et al., 2003; Renzi & Johnson, 2007; Abdel-Aal et al., 2013; Mrowicka et al., 2022; Li et al., 2023 for reviews of germane evidence). Beyond the preservation of health, L+Z play a significant role in static and dynamic visual performance. MP contributes to improved functional vision by improving chromatic contrast (Renzi & Hammond, 2010a), reducing glare disability and discomfort (Stringham et al., 2003; Stringham & Hammond, 2007b), shortening photostress recovery time (Stringham et al., 2011), and extending visual range (Wooten & Hammond, 2002; Fletcher et al., 2014). However, the advantages of L+Z are not limited to sustained eye health and augmented anterior optics, as they also promote cognitive performance and processing efficiency.

Extant data strongly suggest that L+Z improve processing speed and temporal vision. CFF thresholds provide a measure of temporal contrast sensitivity at 100% temporal contrast (Wooten et al., 2010). This upper threshold for flicker perception is determined by a network of brain structures and depends on factors such as attentional resources (Mankowska et al., 2022). CFF is a reliable indicator of dynamic visual and cognitive function (Wooten et al., 2010; Saint et al., 2021). This visual biomarker has been demonstrated to have a strong positive relationship with MPOD (Hammond & Wooten, 2005; Renzi & Hammond, 2010b). Renzi & Hammond originally posited the Neural Efficiency hypothesis, which postulates that L+Z improve processing speed and reduce neural noise (2010b). Additionally, MPOD has been related to significantly accelerated reaction times, improved balance ability, and reduced errors in a coincidence anticipation task (Renzi et al., 2013).

Since central nervous system L+Z (measured as MPOD) change as dietary L+Z changes, interventional studies assessing causality are possible. Randomized placebo-controlled trials (RCT) of L+Z supplementation have demonstrated improvements in higher-order cognitive performance and neural efficiency. In a 2017 RCT, for example, L+Z supplementation increased MPOD and was related to improved cognitive function (as measured via computerized multi-domain neuropsychological tests) in young, healthy adults (Renzi-Hammond et al., 2017). A 2019 RCT investigated the effects of L+Z supplementation on cognitive performance, and the treatment group demonstrated a significant increase in MPOD that was significantly correlated to improvements in both processing speed and psychomotor speed (Stringham et al., 2019). Oliver et al. (2019) and Ceravolo et al. (2019) both showed that higher MPOD was related to differences in brain activation as measured by steady-state visual evoked potentials, a possible indication of improved signal-to-noise ratios of neural activity. MPOD appears to be directly linked to the efficiency and sensitivity of the fast-motion system (Bovier et al., 2014; Bovier & Hammond, 2015).

The Possible Effect of Lutein and Zeaxanthin on the Slow-Motion System

Although the effects of L+Z have been well-studied for the fast-motion system, no data currently exist regarding how L+Z influence the slow-motion system. Such effects are not obvious. Slow-motion detection is largely determined via serial activation of retinal neurons (Lappin et al., 2009) and MP is not uniformly distributed across the retina. This serial activation is based on the optical fidelity of the stimulus: for example, Leibowitz and colleagues investigated the effect of stimulus eccentricity and refractive error on slow-motion sensitivity, and they found that sensitivity decreased with eccentricity (i.e., threshold increased in the far periphery by a factor of 6 compared to central foveated vision), and the presence of individual

differences in threshold disappeared when refractive error was corrected (1972). These results (albeit on only three participants) strongly imply that slow-motion perception is highly dependent upon the optical fidelity of the retinal image. In other words, if an image is blurred, it will be less able to discretely activate adjacent neurons (Leibowitz et al., 1972). Unlike more anterior filters (such as those found in fish and birds; Walls & Judd, 1933), MP influences optical scatter only in and around the fovea. This could have incidental costs. The presence of higher concentrations of L+Z in the central retina (i.e., higher MPOD) produces an inconsistency in screening. Consistent incoming visual information is crucial in the construction of a coherent visual experience. The non-uniformity in screening leads to differences in compensatory gain in the central and peripheral visual fields as a means of maintaining perceptual balance (Stringham & Stringham, 2015). Differences in screening due to the presence of MP can substantially influence visual sensitivity (Hammond et al., 1998). These issues all suggest the real possibility that MP may influence slow-motion thresholds in a manner that is different than how central L+Z influences fast-motion detection.

Considerations for This Investigation

In this study, we measured slow-motion thresholds using a customized system designed to optimize ecological validity. These thresholds were then compared to L+Z status quantified as MPOD (as well as a few other easily assessed variables analyzed as exploratory outcomes). The system used to measure slow motion was based on combining a xenon-based optical system with fiber optic leads and a computer-controlled slide to move the stimulus smoothly and precisely. Thresholds were determined using classical psychophysical procedures that were adapted to this system (for details of this apparatus and procedure, see Chapter 2). This apparatus/procedure was used to quantify the functional limit of an individual's slow-motion system: an isochronal

threshold (as termed by Leibowitz et al., 1972) for the detection of rectilinear translational motion (also termed the lower threshold of motion, LTM). In essence, LTM is the slowest velocity at which an individual can detect a physical change in location when the duration of the exposure is kept constant.

To evaluate the relationship between slow-motion and L+Z status, several components of the experimental design were considered. MPOD was measured using customized heterochromatic flicker photometry (for details of this methodology, see Chapter 2). To disentangle the possible optical (i.e., filtration) and physiological (i.e., cortical) effects of L+Z, LTM was measured centrally (where MP is most dense) and peripherally (where there is no measurable MP), and the wavelength composition of the LTM stimuli was varied. The apparatus and design originally used by Leibowitz and colleagues (1972) served as the conceptual basis for our LTM measures.

Threshold Considerations

A sensory threshold is the probabilistic intensity value at which a stimulus either becomes detectable or stops being detectable. To calculate a threshold for detection in a forced choice procedure, a given detection rate must be chosen, where at rates above this detection percentage the observer is thought to perceive the stimulus, and at rates below this detection percentage the observer is thought to not perceive the stimulus.

The probabilistic nature of perception, especially for complicated tasks such as motion perception, requires that a given percentage correct criterion for detection be lower than 100%. Different detection rates are used to establish threshold criteria depending on the sensory stimulus and the psychophysical procedure used. A common percentage used for threshold criterion in visual detection tasks is 77.5% (e.g., Boulton, 1987). To achieve a rate of correct

detection above this value demonstrates a high level of confidence in the observer's perception. A high criterion is usually used when testing the limits of a perceptual phenomenon that is reasonably well understood.

In this investigation, detection thresholds were calculated using a 50% correct criterion, corresponding with the precedent set by Leibowitz et al. (1972). During informal preliminary testing in the construction of the LTM device and procedure (for details of device and procedure, see Chapter 2), higher rates of motion detection for 1-second stimulus exposures were observed to be less than consistent (70-80%) even for relatively fast speeds (>20-arcmin/sec). Even at the fastest velocity (~47-arcmin/sec) that the stimulus could travel, detection rates of 100% were not consistently acquired; this indicated wide variability in slow-motion perception between individual observers. Given these rates of correct detection, it was determined that the complexity of the stimulus and the noisy nature of the motion-perception system required threshold values that more closely aligned with the 50% correct precedent set by Leibowitz and colleagues (1972) rather than the 77.5% used by Boulton (1987).

Stimuli Considerations

The findings of any psychophysical investigation are limited by the applicability of the experimental conditions. To achieve applicability to the outside world, the ecological validity of the stimuli used was prioritized. Instead of using common stimuli for motion perception quantification, such as gratings and plaids (e.g., Wright & Gurney, 1992), we opted for diffuse light stimuli that resemble lights often seen in the outside world (e.g., glare from sunlight or automobile headlights).

Optics were emphasized in this investigation because one of Leibowitz and colleagues' main conclusions was that refractive error was a main limiting factor in peripheral slow-motion

sensitivity (1972). To incorporate the effect of dioptric factors, a point source of light and diffuser screens were used in the creation of the light stimuli for the slow-motion apparatus. This diffuse stimulus was useful in examining the effect of optical filtration by MP. It also enhanced environmental validity because stimuli in daily life are often seen because they reflect or emit light (computer screens, headlights, emergency vehicles, bioluminescence, etc.). Leibowitz et al. (1972) for example, used one-second exposures, a fixation point, and a stimulus that was essentially a white (highly reflective) square.

The use of a broadband stimulus condition and a mid-wavelength stimulus condition (for details regarding the wavelength composition of these stimuli, see Stimuli for Slow-Motion in Chapter 2), in conjunction with central and peripheral measurements, enabled the examination of the effect of L+Z status on LTM. Broadband light from a xenon-arc lamp was used as the light source of the stimulus because the spectral distribution closely replicates that of mid-day sunlight (e.g., Figure 1 of Hammond et al., 2013). Two stimulus conditions, broadband (xenon broadband passed through a "blue-sky" interference filter) and mid-wavelength (xenon broadband passed through a 574-nm interference filter), were used. The broadband skylight stimulus was used because it represents commonly encountered light during the day and because MP filters short-wavelength light. The mid-wavelength light stimulus was used because 574-nm light corresponds to peak sensitivity in the normative human visual system, and unlike the short-wavelength dominant broadband stimulus, it was unaffected by MP filtration. Central and peripheral measurements were used to differentiate the optical and physiological effects of L+Z. MP is only present in measurable quantities in the central 5-degrees of the retina (Snodderly et al., 1984), so any relationship between MPOD and LTM found in the central visual field but not the peripheral visual field in the broadband condition could be attributed to the filtration of

shortwave light by MP in the retina. Further, any relationship between L+Z status found in the peripheral visual field but not in the central visual field could be attributed to the cortical effects of L+Z (e.g., neural efficiency; Renzi & Hammond, 2010b).

Experimental and Sample Considerations

When considering the size of the sample used to investigate the relationship between LTM and L+Z status, preliminary results from an informal pilot study on lab personnel suggested that a sample size with as few as 9 participants was sufficient to assess the statistical nature of the effect. Given this and the desire to assess participants under various stimulus conditions, the overall sample size was set to 40 individuals (15 receiving LTM measurement in broadband stimulus only, 15 receiving LTM measurement in mid-wavelength stimulus only, and 10 receiving LTM measurement in both stimulus conditions).

To measure LTM under optimal neurological conditions and to isolate the possible effect of L+Z status, we sought to measure young, healthy people with good vision without needing visual correction. Consequently, participants between 18 and 30 years of age were tested. The utilization of a sample of young, healthy people enabled the measurement and characterization of motion perception performance under optimal conditions (e.g., efficient neurological processing and non-dense crystalline lens). Participants must also have been able to conduct the psychophysical tasks without added visual correction. The exclusion of individuals that required corrective lenses (i.e., 20:45 binocular Snellen visual acuity or worse) minimized the influence of refractive error (which is thought to diminish motion perception sensitivity; Leibowitz et al., 1972). The exclusion of individuals wearing corrective spectacles or contact lenses was intended to reduce possible confounding for better (blur or additional scatter can sometimes be used as a motion cue) or worse. Further, with the rising popularity of photochromic and other lenses with

light-filtering additives, the exclusion of additional lens media prevented any influence of confounding light filters. Finally, participants were required to have good uncorrected vision (i.e., 20:40 monocular Snellen visual acuity or better) in their right eye (O.D.) to participate, as the alignment of the system was optimal for use with the right eye.

CHAPTER 2

METHODS

Participants

For this investigation, participants were recruited from the undergraduate student population through the University of Georgia's SONA system for research credit. Participants were also recruited from the local Athens-Clarke County, GA community on a word-of-mouth basis. A total of 60 potential participants signed up to participate. Participant attrition from the recruitment stage to the enrollment stage was high, as 20 of the 52 individuals recruited on the SONA platform were not successfully enrolled in the study. This was due to either failing to arrive to the testing site (70%) or failing to meet eligibility criteria (30%).

Inclusion criteria included fluency in written and spoken English, age between 18 and 30 years of age, uncorrected visual acuity of 20:40 or better monocularly (O.D.) and binocularly (O.U.), the ability to sit for 40 minutes without breaks, the ability to see the stimuli without ancillary vision correction, and good ocular health at the time of last eye exam. Exclusionary criteria included the presence of medical or eye conditions, extreme sensitivity to light, or failure to meet any of the inclusion criteria.

All participants who arrived at the testing site and met eligibility criteria were enrolled in the study and completed data collection. Three enrolled participants were excluded from data analysis because they failed to reliably perceive the test stimulus or did not attend to the test stimulus during testing; therefore, their threshold value for motion detection sensitivity could not

be accurately determined. Forty young, healthy participants were measured, yielding a final analyzable sample of 37.

Demographics

The final analyzable data set included 37 healthy participants ranging from 18-27 (*M* = 19.32 ± 1.97) years of age with the majority being female (N = 27 female, 10 male). Approximately 86% of the sample was White; 5% Black; 5% Asian/Pacific Islander; and 3% Multiracial. All participants had 20:40 or better uncorrected visual acuity in both eyes (O.U.) and right eye (O.D.). In the final analyzable sample, 22 participants were right-eye dominant (O.D.; 59%), and 15 participants were left-eye dominant (O.S.; 41%).

Ethics Statement

All participants provided verbal and written informed consent prior to participation. The tenets of the Declaration of Helsinki were adhered to at all times during the course of the study. The protocol and all study materials were approved by the University of Georgia's Institutional Review Board (PROJECT00007466).

Study Design

See **Figure 1** for a flowchart of participation. CFF and MPOD were measured for all participants at each visit. Each participant was also measured for central LTM (foveated visual field) and peripheral LTM (~33 degrees of retinal eccentricity). The wavelength composition of the LTM stimulus was varied to examine the effect of MP filtration. The order of central and peripheral LTM measurement was randomized by flipping a coin for each participant (62% peripheral first, 38% central first). Upon enrollment, participants were randomized into three groups: a group whose central and peripheral LTM were measured using a broadband stimulus condition, a group whose central and peripheral LTM were measured using a mid-wavelength

(574-nm) stimulus condition, and a group that was measured using both conditions in two visits, 1-14 days apart. Of the 37 participants in the final analyzable data set, 14 participants had their CFF, MPOD, and broadband stimulus condition central and peripheral LTM measured, 13 participants had their CFF, MPOD, and mid-wavelength stimulus condition central and peripheral LTM measured, and 10 participants had their CFF, MPOD, and LTM and central and peripheral measured under both stimulus conditions.

Slow-Motion Apparatus

The apparatus that was used to measure LTM consisted of a one-channel optical system combined with a computer-controlled translation slide. This system is shown in the schematic presented in **Figure 2**. A 1000-watt xenon arc-lamp (Newport Corporation; Irvine, CA) was used as the light source. The light was passed through a collimating lens, a water bath (for heat removal) with a 10-mm x 10-mm exit aperture, a 250-mm focal length focusing lens, a "blue-sky" interference filter (Midwest Optical Systems, Inc.; Palatine, IL) for the broadband stimulus condition or a 574-nm interference filter (Newport Corporation; Irvine, CA) for the mid-wavelength condition, and a shutter-controlled aperture before traveling down a fiber optic cable attached to a computer-controlled translation slide. The spectral compositions of these two light stimuli are presented in **Figure 3**. The stimulus light then exited the fiber optic cable through a 6-mm aperture, traveled 40-mm to a 5-mm thick diffuser screen, and then traveled 845-mm from the diffuser screen to the eye of the observer.

A forehead/chinrest assembly was used to stabilize participants' heads. A small (~4-mm) red LED fixation point (570-mm to the participant's left and on the same plane as the stimulus aperture; visual angle of approximately 33-degrees) was used to stabilize the participant's gaze. This fixation light was placed behind the diffuser screen for the peripheral LTM task. For the

central fixation condition, a small (10-mm x 10-mm) red square of paper on the diffuser screen directly in front of the observer was used (this square appears just under the stimulus). The central fixation aid was intended to provide a stable location for participant viewing while waiting for the foveal stimulus exposure as the slide crossed in front of the participant.

Stimuli for Slow-Motion

The broadband stimulus (see **Figure 3**) consisted of a relatively bright (~633-lux) white light from the xenon lamp light source passed through a blue-sky filter to approximate outdoor (i.e., ecologically valid) conditions. This stimulus aperture of 6-mm subtends approximately 23-minutes of visual angle. The mid-wavelength stimulus (see **Figure 3**) consisted of the same broadband light from the xenon lamp light source passed through a 574-nm interference filter. This waveband is at peak sensitivity for the normative human visual system and is not absorbed by MP. The stimulus aperture in the peripheral condition remained the same size as the broadband condition, but the intensity of the mid-wavelength stimulus (~90-lux) was less than the broadband stimulus, due to the different interference filters used.

Procedure for Measuring Slow-Motion

Measurements were conducted monocularly in each participant's right eye only (O.D.), irrespective of ocular dominance. A soft black adjustable eye patch was used to completely cover and occlude their left eye (O.S.). The eye patch strap was adjusted to maximize comfort and to ensure the strap did not impinge upon participants' right eyelids or affect their fields of view. To assess the possible influence of ocular dominance on LTM, ocular dominance was recorded.

To measure LTM, a modified method of limits was used to bracket the zone of uncertainty (~50% correct detection). The velocity of the stimulus was the independent variable. The stimulus was moved at varying precise speeds using a computer-controlled translation slide

(Velmex, 12-inch linear stage motorized Xslide, velmex.com). For each trial, the stimulus was exposed for 1-second while traveling at a constant velocity between 0.2-arcmin/sec and ~47-arcmin/sec. Exposure was triggered by the experimenter as the fiber optic cable aperture mounted on the translation slide crossed directly in front of the participant.

The participants responded to each trial with a "yes" (affirmative) or "no" (negative) to indicate whether they detected any movement of the stimulus. This forced-choice task required participants to respond either "yes" or "no," and if the participant responded "yes," then they were also asked to report the direction (left or right) of the perceived movement. Trials in which participants reported affirmative detection of movement and the correct direction were recorded as successful detection; whereas, trials in which participants responded "no" and trials in which the participant incorrectly judged the direction of movement were recorded as no motion successfully detected. Participants were provided with an identical encouraging verbal response from the researcher following every trial to help maintain their confidence, despite the accuracy of their judgment.

To orient the participant to the task, two initial exposures were demonstrated: the first without movement (i.e., stationary, 0-arcmin/sec) and the second with fast movement (~47-arcmin/sec). Once these preliminary demonstrations were completed, the experimenter used descending velocities (starting around 47-arcmin/sec and decreasing by 2.4-arcmin/sec) and ascending velocities (starting around 0.2-arcmin/sec and increasing by around 1.2-arcmin/sec) to determine the range of the participant's zone of uncertainty. The experimenter asked the participant to take a break and rest their eyes after every five trials to avoid fatigue. At fast speeds well above their LTM, participants easily responded "yes" to the detection of movement. At slow speeds well below their LTM, participants easily responded "no" to the detection of

movement. When approaching speeds near threshold, judgments became more difficult, and their responses became less certain. When the descending velocities began to elicit a negative response from the participant and the ascending velocities began to elicit an affirmative response from the participant, the range of velocities that encompass a given participant's LTM was considered identified. This range of velocities (i.e., zone of uncertainty) was typically between 2.5-arcmin/sec and 7-arcmin/sec in breadth. Once the range of velocities within the zone of uncertainty was identified, a staircase procedure was used to determine the average velocity at which the participant reported the perception of movement at a 50% detection level. LTM values were calculated by averaging the velocities of 10 trials in this range.

Sub-Sample Investigation of Peripheral Slow-Motion Sensitivity

A subset (n = 3) of participants were tested more extensively to more fully characterize the psychometric function generated by our procedure in the peripheral broadband stimulus condition. The method used remained largely the same, but the method of constant stimuli was used instead of the modified method of limits and staircase methodology. There were several reasons for this adjustment in methodology. There were not the time constraints present in the measurement of the LTM in the larger sample. The participants that chose to return for peripheral LTM testing were highly motivated and engaged. These three participants also had practice with the procedure. For each of the three participants, numerous trials were conducted (an average of 154 trials per participant). Each trial had a constant stimulus velocity between 0.2-arcmin/sec and ~47-arcmin/sec. Velocities were grouped into ranges of 2.44-arcmin/sec, and sensitivity was determined by the number of correct trials detected within that range divided by the total number of trials within that range.

Sensitivity curves were plotted for each of the three participants, an aggregate sensitivity curve was created by combining all three participants' trials for each velocity range, and an average sensitivity curve was created by averaging all three participants' sensitivity within each velocity range. To determine which function best described the relationship between peripheral motion sensitivity and stimulus velocity as represented by the aggregate and the average data, R^2 values were compared for a variety of possible functions using Microsoft Excel (Version 16.80). LTM for each of the participants in the sub-sample was calculated using the power function fit to their sensitivity data.

Macular Pigment Optical Density

For details regarding the measurement and validity of MPOD assessment via customized heterochromatic flicker photometry (cHFP) see Wooten et al. (1999) and Hammond et al. (2005). MPOD was assessed in each participant's right eye only (O.D.), using a soft black adjustable eye patch to completely cover and occlude their left eye (O.S.).

cHFP is considered customized because the measurement of MPOD is adapted to the individual being measured; specifically, flicker rates are optimized to enable narrow (and hence, the most accurate) flicker fusion frequency regions. Critical flicker fusion frequency (CFF) thresholds were measured prior to MPOD to calibrate the system to each individual's sensitivity to flicker. To measure CFF, the test stimulus consisted of a circular 1-degree test field composed of 570-nm light. The CFF test stimulus flickered with 100% square-wave modulation, and the intensity of the stimulus when on (~0.5-cd/m^2) was held constant. The rate of flicker started at 5 to 10-Hz and was increased until the participant reported the test stimulus appeared solid (i.e., flicker fusion), once this occurred, the rate of flicker was set to approximately 35 to 40-Hz and decreased until the participant reported perception of flicker returning. Three ascending and three

descending measures were conducted for each participant. The resulting frequency values were averaged to yield a CFF value for the participant.

The test stimulus for MPOD measurement consisted of a circular 1-degree stimulus for the foveal condition (yielding measurements at 30-arcmin) and was viewed in free-view using a 5-arcmin spot located in the center of the target as a fixation point. The test stimulus alternated between 458-nm (measuring stimulus, peak absorption by L+Z) and 570-nm (reference stimulus, no absorption by L+Z) in a square-wave phase. The intensity of the test stimulus (~3.0-cd/m^2) was held constant through yoking the intensities of the measuring and reference components of the stimuli. This test stimulus was superimposed onto and presented in the center of a 6-degree, 470-nm circular background. The stimulus alternated between the measuring and reference wavelengths at the optimized flicker rate derived from their CFF value. The yoked intensities of the test stimuli were adjusted until the participant indicated that they perceived the test stimulus as fused (non-flickering). The relative intensities were then recorded. For the parafoveal condition, the fixation point instead consisted of a 5-arcmin red spot located 7-degrees to the left of the test stimulus. At 7-degrees of retinal eccentricity, there is no optically measurable L+Z and subsequently negligible filtration by MP; therefore, the parafoveal measure provided a control against which the centrally located foveal measure was compared. The test stimulus and procedure remained the same as the foveal measurement other than the retinal location (7-degrees of arc) and size (2-degrees of arc) of the stimulus.

For each participant, the relative intensities at which the perception of flicker disappears were obtained five times in each retinal location (i.e., five measurements were conducted in the fovea and five measurements were conducted in the parafovea). Each set of scores was averaged together to represent the relative energy necessary for flicker fusion in the fovea and parafovea.

MPOD was derived from the difference between the log relative energy necessary for flicker fusion in the fovea vs. the parafovea.

Analyses Conducted

RStudio (Version 2023.09.1+494) was used to conduct all statistical analyses described below. Given the exploratory nature of this study, both tails of the distribution were tested, with statistical significance at $p < 0.05$ and trends of $p < 0.1$ noted. Pearson's product-moment correlations were computed to assess the relationships between continuous variables, such as MPOD and LTM, in both the broadband stimulus condition and the mid-wavelength stimulus condition. Point-biserial correlation coefficients were computed to assess the relationships between dichotomous and continuous variables, such as ocular dominance and LTM. Paired samples t-tests were computed to assess the degree of difference between variables in the within-subjects data (i.e., participants who participated in two visits, one for each LTM stimulus condition). Welch two independent samples t-test were computed to assess the degree of difference between variables (e.g., central LTM, peripheral LTM, and difference between central and peripheral LTM) in separate groups (e.g., those differing by condition, ocular dominance, etc.). Microsoft Excel (Version 16.80) was used to assess the function that best described the slow-motion curves created using the method of constant stimuli.

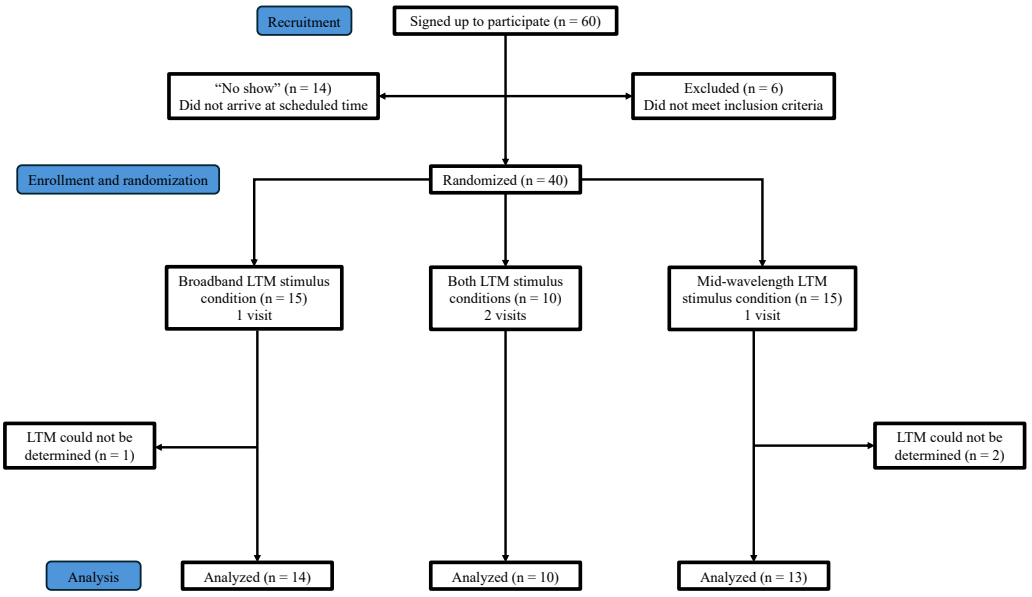

Figure 1

Flowchart of Participation

Note. The lower threshold of motion (LTM).

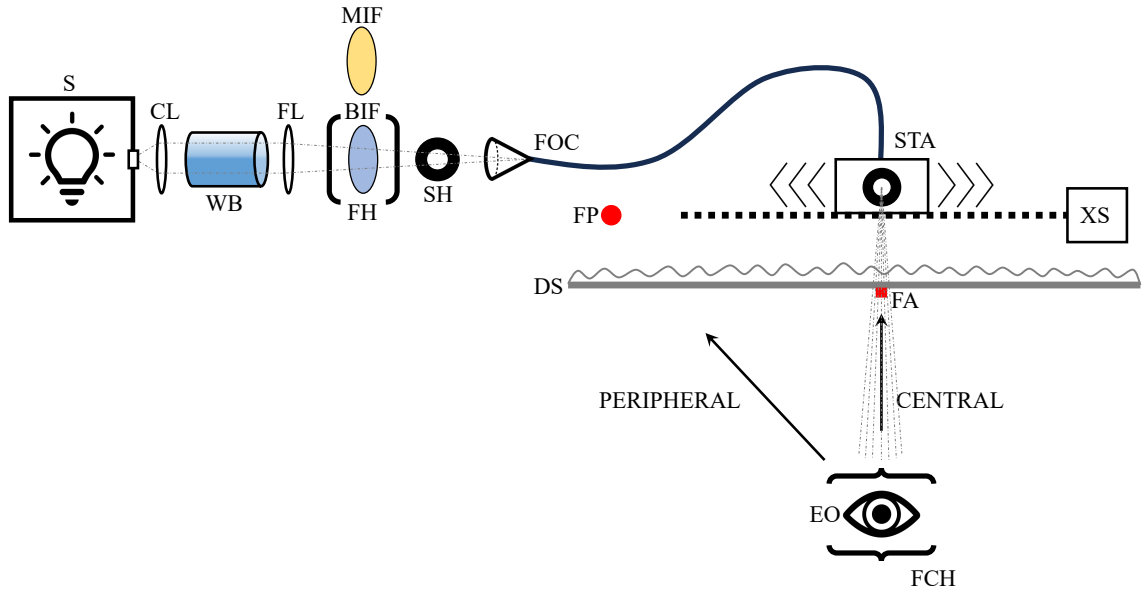

Figure 2

Schematic of the Slow-Motion Apparatus

Note. A schematic of the slow-motion apparatus. S, xenon arc light source; CL, planoconvex achromatic collimating lens; WB, water bath for heat removal; FL, 250-mm focal length planoconvex focusing lens; MIF, 574-nm interference filter; BIF, blue-sky interference filter; FH, filter holder; SH, shutter-controlled aperture; FOC, fiber optic cable; STA, 6-mm stimulus aperture; XS, computer-controlled translation slide; FP, peripheral fixation point; DS, 5-mm thick diffuser screen; FA, central fixation aid; EO, eye of the observer; FCH, forehead/chinrest assembly. Path of light is shown in light grey. Not to scale; see Chapter 2 “Slow-Motion Apparatus” for spacing details.

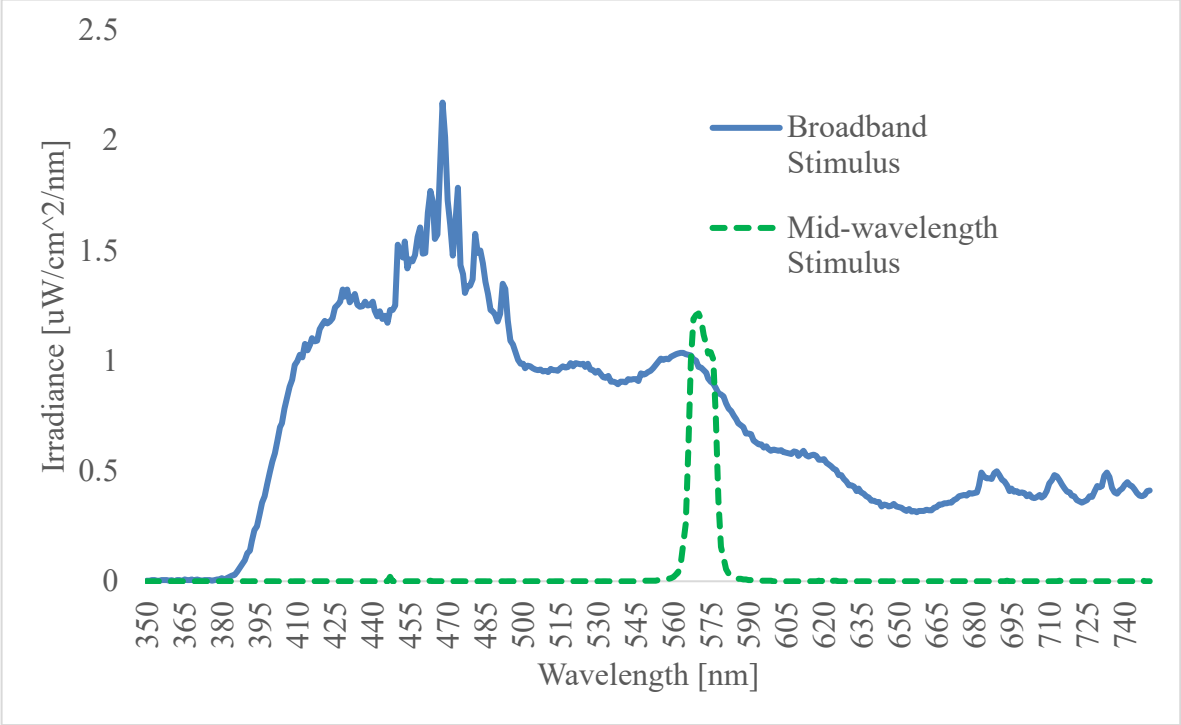

Figure 3

Spectral Composition of Slow-Motion Stimuli

Note. Spectrum of visible light emitted from the slow-motion apparatus with "blue-sky" interference filter (broadband stimulus) and 574-nm interference filter (mid-wavelength stimulus). Measurements were taken at the diffuser screen.

CHAPTER 3

RESULTS

Individual Differences

The LTM scores demonstrated both the ability of the human visual system to detect minuscule motion of a stimulus across the retina and dramatic individual differences in this ability. Measurements were conducted with two stimulus conditions (broadband and mid-wavelength) and in two retinal locations (central and peripheral). See **Table 1** for the mean, standard deviation, minimum, maximum, and range of LTM under each measurement condition. Central LTM in the broadband condition (*M* = 11.73-arcmin/sec, *SD* = 8.57) ranged from a maximum of 32.99-arcmin/sec to a minimum of 0.65-arcmin/sec (by a factor of 50.75). This standard deviation represents 73% of its mean. Peripheral LTM in the broadband condition (*M* = 13.26-arcmin/sec, *SD* = 10.72) ranged from a maximum of 38.90-arcmin/sec to a minimum of 1.00-arcmin/sec (by a factor of 38.9). This standard deviation represents 81% of its mean. Central LTM in the mid-wavelength condition (*M* = 9.84-arcmin/sec, *SD* = 7.38) ranged from a maximum of 24.69-arcmin/sec to a minimum of 0.54-arcmin/sec (by a factor of 45.72). This standard deviation represents 75% of its mean. Peripheral LTM in the mid-wavelength condition (*M* = 14.15-arcmin/sec, *SD* = 9.06) ranged from a maximum of 32.99-arcmin/sec to a minimum of 1.69-arcmin/sec (by a factor of 19.52). This standard deviation represents 64% of its mean. LTM scores in all four measurement conditions varied dramatically (on average ranging by a factor of 38.72) across individuals despite similar age, refractive state, sex, etc. In contrast, CFF in the same sample (*M* = 24.74-Hz, *SD* = 1.97) ranged only from a maximum of 27.8-Hz to a

minimum of 20.5-Hz, or by a factor of 1.36. The standard deviation of CFF scores represents only 8% of its mean.

Lutein and Zeaxanthin and Slow Motion

Despite the well-established relationship between MPOD and the fast-motion system, there were no relations between MPOD and LTM in either stimulus condition or either retinal location. Pearson's product-moment correlations were computed to investigate the relationship between MPOD and LTM in the broadband condition. In the broadband condition, MPOD and central LTM were not significantly related ($r(22) = -0.15$, $p = 0.48$), MPOD and peripheral LTM were not significantly related ($r(22) = 0.05$, $p = 0.83$), and MPOD and the difference between central and peripheral LTM were not significantly related ($r(22) = -0.18$, $p = 0.40$). Pearson's product-moment correlations were also computed to investigate the relationship between MPOD and LTM in the mid-wavelength condition. In the mid-wavelength condition, MPOD and central LTM were not significantly related ($r(21) = 0.03$, $p = 0.88$), MPOD and peripheral LTM were not significantly related ($r(21) = -0.10$, $p = 0.65$), and MPOD and the difference between central and peripheral LTM were not significantly related ($r(21) = 0.15$, $p = 0.48$). MPOD was unrelated to all LTM metrics in both stimulus conditions.

Ancillary Analyses

Ancillary analyses were also conducted for exploratory purposes. Several significant relationships were identified during this phase of analysis, yet these were not part of our *a-priori* hypotheses.

Ocular dominance (i.e., whether the participant used their dominant or non-dominant eye as test eye) was significantly related to slow-motion perception in several ways. Using a point-biserial correlation, ocular dominance was found to be significantly correlated with central LTM

in the mid-wavelength condition, $r(21) = 0.45$, $p = 0.03$. However, when assessing the degree of difference in central LTM between individuals using their dominant eye (n = 15, $M = 7.49$) and those using their non-dominant eye (n = 8, $M = 14.25$), the result of the independent samples t-test demonstrated that the degree of difference between groups was not significant but was trending toward significance ($t(21) = -2.00$, $p = 0.07$). Ocular dominance was also found to be significantly correlated with the difference between central and peripheral LTM in the mid-wavelength condition, $r(21) = 0.44$, $p = 0.03$. An independent samples t-test revealed that the difference between central and peripheral LTM was significant ($t(21) = -2.60$, $p = .02$) in participants using their non-dominant eye (n = 8, $M = 0.09$) compared to those using their dominant eye (n = 15, $M = -6.65$). Additionally, in the mid-wavelength condition among participants that used their dominant eye (O.D.), central LTM scores ($M = 7.49$) were significantly different than peripheral LTM scores ($M = 14.14$), $t(14) = -3.40$, $p = 0.004$. Whereas, individuals using their non-dominant eye in the same conditions demonstrated no such relationship, $t(7) = 0.05$, $p = 0.96$.

The relationship between CFF and LTM was investigated using Pearson's product-moment correlations. The difference in central and peripheral LTM in the mid-wavelength condition was significantly correlated with CFF, $r(21) = -0.42$, $p < 0.05$. This indicates that individuals with higher CFF had worse peripheral LTM compared to their central LTM. See **Figure 4** for a visual representation of this relationship.

In the broadband condition, both central LTM and peripheral LTM significantly differ between males and females. The degree of difference between males' average central LTM (n = 8, $M = 6.98$) and females' average central LTM (n = 16, $M = 14.10$) was found to be significant ($t(22) = -2.43$, $p = 0.02$) in the broadband condition. Additionally, the degree of difference

between males' average peripheral LTM (n = 8, $M = 4.98$) and females' average central LTM (n = 16, $M = 17.40$) was found to be significant ($t(22) = -3.90$, $p < 0.001$). However, no such relationship was found in the mid-wavelength condition when the degree of difference between males and females was examined for central LTM ($t(21) = -1.21$, $p = 0.26$) and peripheral LTM ($t(21) = -0.83$, $p = 0.43$).

In participants that were measured in both stimulus conditions, the degree of difference between their central LTM in the mid-wavelength condition and their central LTM in the broadband condition was found to trend towards significance ($t(9) = -2.16$, $p = 0.06$).

Sub-Sample Investigation

The sub-sample investigation into broadband peripheral LTM using the method of constant stimuli enabled the description of the relationship between broadband slow-stimulus velocity and peripheral detection of motion at slow speeds. According to the R^2 values of the aggregate ($R^2 = 0.94$) and average ($R^2 = 0.97$) motion curves, a power function best describes the relationship between these variables (see **Figure 5** and **Figure 6**). Power functions derived from the aggregate and average sensitivity data were used to calculate threshold values at 50% detection rates, yielding a peripheral LTM of 10.13-arcmin/sec for the aggregate curve and a peripheral LTM of 9.66-arcmin/sec for the average curve.

The slow-motion and sensitivity data from each participant in the sub-sample investigation were also plotted, and a power function was fit to the data (see **Figures 7**, **8**, and **9**). These power functions were used to calculate threshold values at 50% detection rates for each participant (001: 13.30-arcmin/sec; 005: 7.16-arcmin/sec; 006: 11.44-arcmin/sec). The average of these three peripheral LTM in the sub-sample is 10.63-arcmin/sec and the standard deviation is 3.15. During the primary investigation, participants 001 and 005 were randomized into groups

that were measured for peripheral LTM in the broadband stimulus condition using the modified method of limits and staircase methodology, but their peripheral LTM scores (001: 3.48-arcmin/sec; 005: 1.00-arcmin/sec) did not equate the thresholds derived from the power function via the method of constant stimuli (001: 13.30-arcmin/sec; 005: 7.16-arcmin/sec).

Table 1

Descriptive Statistics for Lower Threshold of Motion Values

Note. Descriptive statistics for lower threshold of motion values in each stimulus condition and retinal location. All values are in arcmin/second.

Stimulus Condition	Retinal Location	Mean	Standard Deviation	Minimum	Maximum	Range
Broadband	Central	11.73	8.57	0.65	32.99	32.34
	Peripheral	13.26	10.72	1.00	38.90	37.90
Mid-wavelength	Central	9.84	7.38	0.54	24.69	24.15
	Peripheral	14.15	9.06	1.69	32.99	31.30

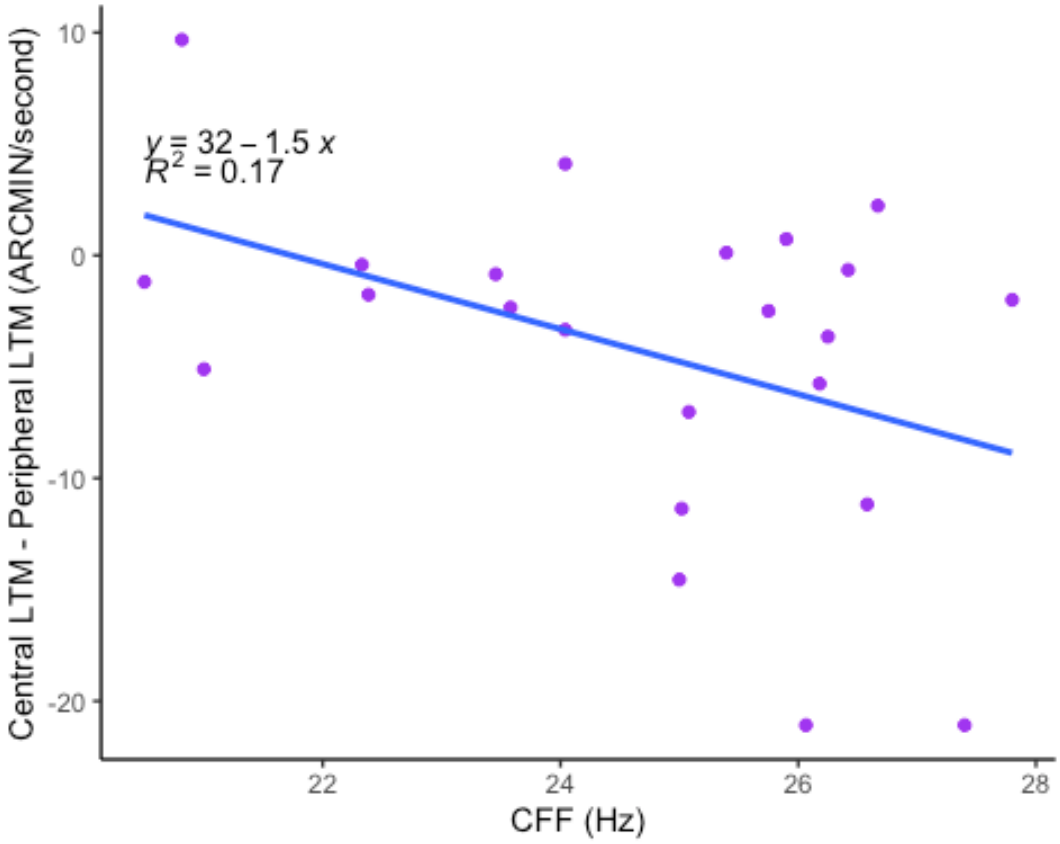

Figure 4

Relationship Between CFF and The Difference Between Central and Peripheral LTM in the Mid-Wavelength Condition

Note. Critical flicker fusion threshold (CFF) was measured in Hertz (Hz); the lower threshold of motion (LTM) was measured in arcmin/second; least squares regression line ($y = 32 - 1.5x$; $R^2 = 0.17$) was plotted to illustrate the nature of the relationship between the two variables.

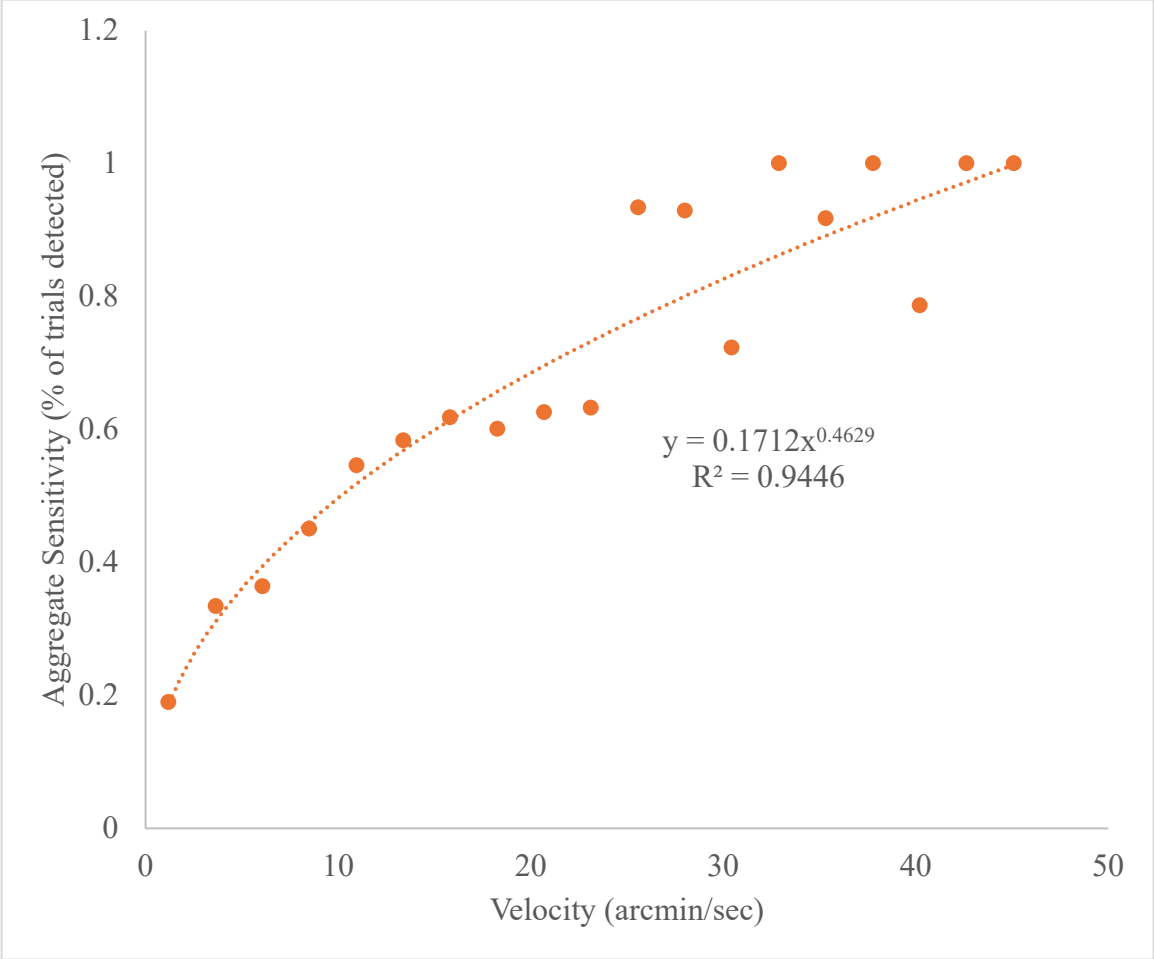

Figure 5

Sub-Sample Aggregate Broadband Peripheral Lower Threshold of Motion Sensitivity Curve

Note. A power function ($y = 0.1712x^{0.4629}$) best fits the data ($R^2 = 0.9446$).

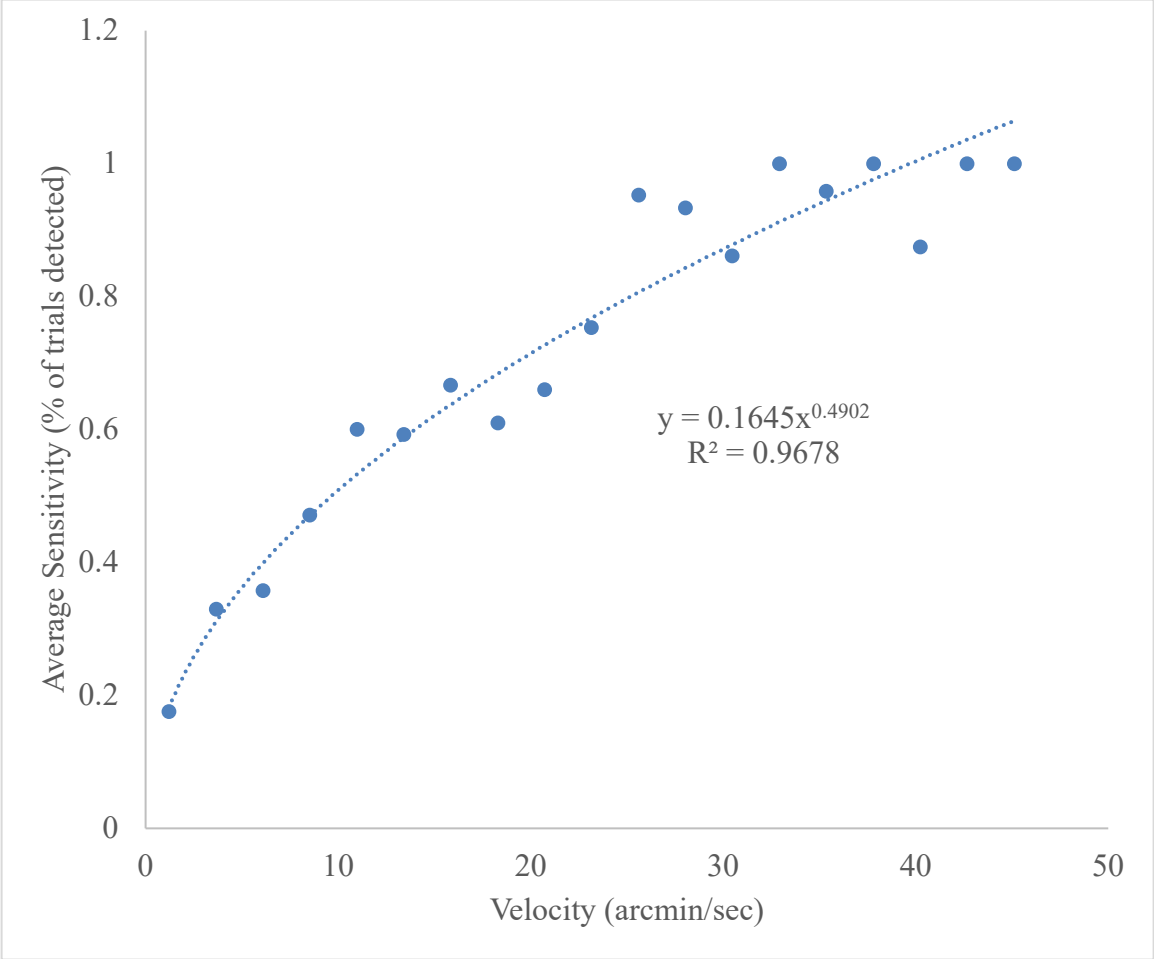

Figure 6

Sub-Sample Average Broadband Peripheral Lower Threshold of Motion Sensitivity Curve

Note. A power function ($y = 0.1645x^{0.4902}$) best fits the data ($R^2 = 0.9678$).

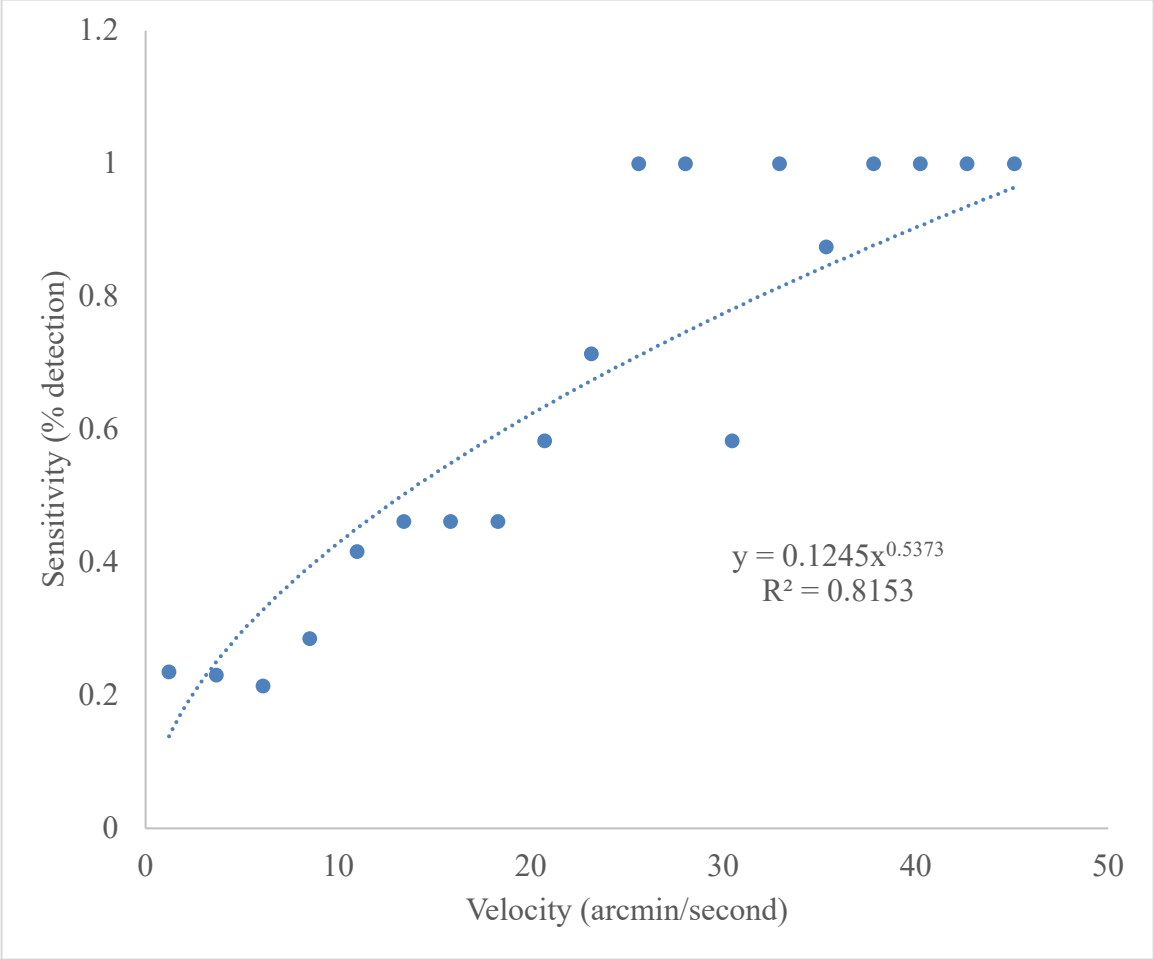

Figure 7

Broadband Peripheral Lower Threshold of Motion Sensitivity Curve for Participant 001

Note. A power function ($y = 0.1245x^{0.5373}$) was fit to the data ($R^2 = 0.8153$).

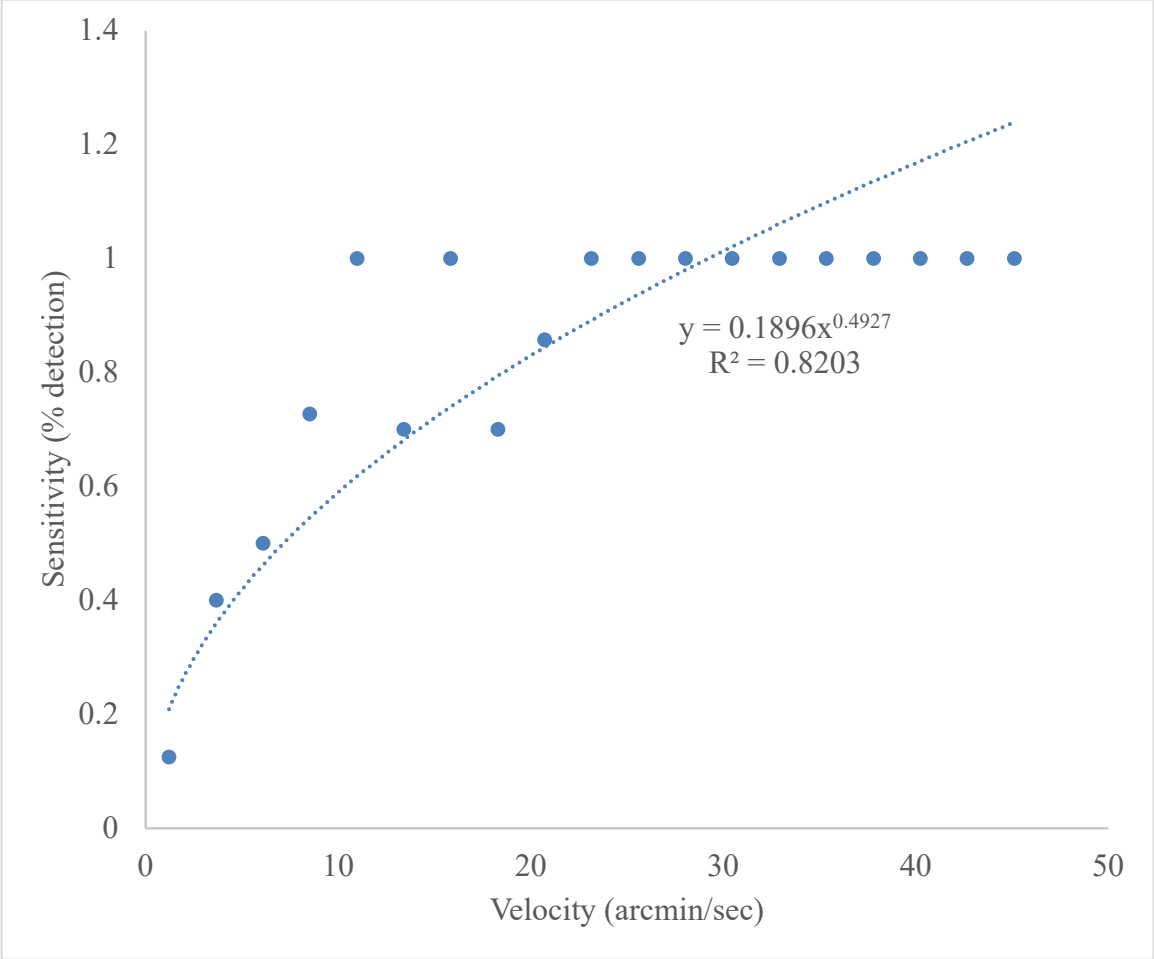

Figure 8

Broadband Peripheral Lower Threshold of Motion Sensitivity Curve for Participant 005

Note. A power function ($y = 0.1896x^{0.4927}$) was fit to the data ($R^2 = 0.8203$).

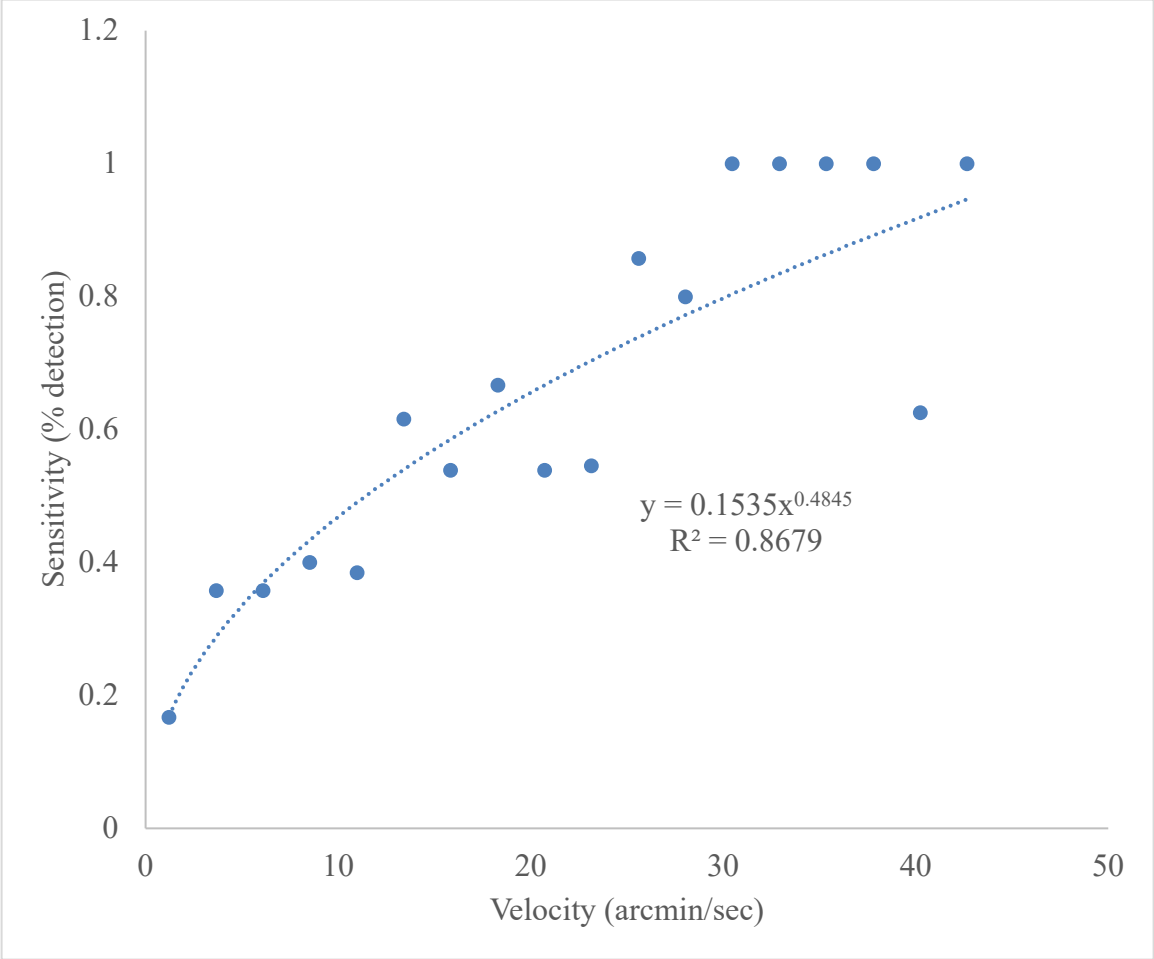

Figure 9

Broadband Peripheral Lower Threshold of Motion Sensitivity Curve for Participant 006

Note. A power function ($y = 0.1535x^{0.4845}$) was fit to the data ($R^2 = 0.8679$).

CHAPTER 4

DISCUSSION

Primary Investigation

In this investigation, we set out to describe the human slow-motion perception system using a novel apparatus and procedure and to determine whether this system was related to MPOD. The results of this investigation indicate that there are dramatic individual differences in LTM even among people who are similar in many ways (e.g., age, refractive state). Further, L+Z status, as quantified by MPOD, appears to be unrelated to LTM both centrally and peripherally.

The percentage of the mean that the standard deviation represented for CFF was dramatically smaller than the LTM scores. All measures of LTM had far more variability than CFF in the same sample. As shown in **Table 1**, the range in LTM values was extreme (over a factor of 30 on average). In contrast, the range in CFF values from the same participants was only about 26%. In other words, if CFF (our proxy measure of fast motion) varied by as much as slow motion, the values would range from about 10 to 300-Hz. The fast-motion and slow-motion systems demonstrating such disparate levels of individual differences, and the lack of any relationship between MPOD and LTM, indicate that the determinates of fast-motion thresholds and slow-motion thresholds are largely distinct.

The lack of a significant relationship between MPOD and LTM does not necessarily mean that L+Z has no influence on the slow-motion system; it does, however, suggest that the individual differences in LTM exceeds any effect of L+Z. Some immediate questions are

prompted by these results: what could account for these dramatic individual differences and what significance do that have for daily visual function?

The finding that LTM is not related to L+Z status is not surprising. As noted earlier, MP creates a discontinuity across the retina that seems unlikely to aid a simple image-retina motion system. In fact, if not actively corrected, this discontinuity would surely affect other visual functions (like color perception or S-cone sensitivity) across the retina. Past studies (e.g., Stringham et al., 2006; Stringham & Hammond, 2007a) have shown that it does not. If the uneven distribution of MP across the retina negatively influenced the serial activation of photoreceptors across the retina, that would be a distinct disadvantage. Evolutionary pressures typically produce traits that are either advantageous or neutral, so the lack of a deleterious effect makes sense.

MP is known to reduce some glare and scattering issues in the central retina (Stringham et al., 2011; Hammond et al., 2013). Higher MPOD should therefore have resulted in the broadband test stimulus having greater optical fidelity as MPOD increased. The finding that MPOD was unrelated to LTM suggests that this improvement in optics was not large enough to drive a relation between the two variables. We measured LTM in a broad-band white and narrow-band green (~574-nm) condition (see **Figure 3**). The broadband condition was about 7 times more intense and included shortwave light which is known to be subject to an increase in higher-order aberrations. Nonetheless, the average thresholds for the two conditions were similar. Collectively, this suggests that, unlike the small (N = 3) study by Leibowitz (1972), LTM thresholds may not be overly sensitive to optical factors (beyond gross refraction). This also makes sense. For example, hyperacuity is similar to LTM in that it is determined by retinal spacing (which is why it is higher in the central retina) but also depends on some level of post-

receptoral processing. Hyperacuity thresholds, however, are unaffected by higher-order aberrations (Reiniger et al., 2019). When doing a vernier acuity task, even if the lines are not crisp, participants can respond to the offset of the blur itself. A similar mechanism may be at work to identify changes in slow motion.

Characterization of Slow-Motion Sensitivity

This was the first study to characterize LTM in a sample of young, healthy participants. One clear observation was simply that, even in this relatively homogenous sample, the amount of individual variability was surprising. Careful testing of the psychometric functions for each participant suggests that the detection curve was well described as a power function. Participants in a sub-sample were tested exhaustively and their individual curves were well predicted (>80% variance explained) using mathematical power functions. In fact, these functions described 97% of the variance when the data was averaged across participants (see **Figure 6**). This aligns with Stevens' 1957 declaration that power functions describe the relationship between psychological and stimulus magnitude for many perceptual phenomena (e.g., brightness; Stevens, 1957). It highlights that, at threshold, LTM is a highly probabilistic (not stepwise) function (note the very gradual slope in **Figure 6**). LTM is a dynamic (calculative) variable. As shown in **Figures 7-9**, there is within-subject variance even when participants are exposed to similar speeds.

One unexpected result was a lack of clear relation between LTM and CFF thresholds. For example, the correlation coefficient between central LTM in the broadband condition and CFF (n = 24) was 0.10, $p = 0.63$. This suggests that the slow-motion and fast-motion systems may not be strongly coupled. This is surprising since the two systems must work in tandem to create a unified experience of global motion. We know that animals can certainly differ in their abilities to see slow and fast motion (e.g., Healy et al., 2013). Some animals (especially small prey

species) have a distinct advantage to seeing fast (a deer fleeing through the woods, a fly avoiding a swat, etc.) but may gain this ability at the expense of seeing slow (perhaps why many predators specialize in slow-motion stalking). Further research studying the relation between the fast- and slow-motion systems is warranted.

Limitations and Methodological Considerations

Given the dynamic nature of the measurement and the inherent difficultly in identifying slow motion, accurate measurement of LTM requires exhaustive psychophysical measurements. The need to generate a psychometric function for each participant makes large-scale testing impractical. Given the inherent noise in this type of dynamic variable, a larger sample may have been able to detect relations that this smaller sample lacked the power to detect.

One reason why we may not have detected relations between MPOD, CFF, and LTM was simply noise in the data. Some noise was clearly internal and "true." Nevertheless, measurement error may have resulted from the nature of the sample. Using young, healthy participants (primarily undergraduate students) allowed for the measurement of LTM in optimally efficient brains, but at the same time, as evidenced by the high rate of "no show" participants and the prevalence of impatience in those participants that did show up, the young sample (who primarily participated for class credit) could have introduced noise into the data that would not be present in the general population under optimal conditions.

Throughout the development and utilization of this method of measuring the detection of moving stimuli, experimenters recorded several qualitative observations. First and foremost, attentional resources played a large role in the task. That is, participants who were distracted were much less likely to report detection of the stimulus. The importance of attention for perception is obvious, and slow-motion perception is no exception. Additionally, it was observed

that individuals with slower LTM (more sensitive) often had a more precise (less wide) zone of uncertainty. Participants who were less sensitive to motion often had wider ranges of speeds where a 50% detection rate was found. This also makes sense intuitively, as those with high sensitivity were likely able to judge perception with higher levels of confidence, and individuals with lower sensitivity were less confident in their judgment.

Additional Findings and Future Directions

A few interesting observations can be made based on the ancillary analyses. First, ocular dominance appears to influence slow-motion perception. In the mid-wavelength stimulus condition, participants using their dominant eye had a greater average difference between central and peripheral LTM than those using their non-dominant eye. Also, among those who used their dominant eye in the mid-wavelength stimulus condition, the central visual field's sensitivity to motion was significantly different than the peripheral visual field (central visual field demonstrated greater sensitivity than peripheral). This result suggests that ocular dominance may influence slow-motion sensitivity between one's eyes and across retinal eccentricity. Second, CFF (which represented the function of the fast-motion system in the central visual field) appears to be related to differences in LTM across the retina. A higher CFF, measured in the central visual field (i.e., central 1-degree), was related to a greater difference between peripheral LTM and central LTM, but only in the mid-wavelength condition (not influenced by MP). This indicates that the fast- and the slow-motion systems, albeit not directly related, do interact. This relationship between CFF and slow-motion perception difference across the retina with the mid-wavelength stimulus is interesting because of the similarities between the wavelength composition of the stimuli used (no relationship was found for the same LTM metric with the broadband stimulus). Third and finally, the results in the broadband condition indicate that males

are significantly more sensitive to motion than females in both central and peripheral visual fields. The presence of these relationships in one stimulus condition but not in the other could indicate this significance is due to type 1 error. Nonetheless, differences in LTM between males and females as well as differences between individuals using their dominant eye and those using their non-dominant eye require further investigation. A within-subjects study where LTM in both eyes was measured and compared would be of particular interest.

Conclusions

This study identified wide individual differences (over a factor of 30) in the slow-motion system of young, healthy participants with similar age and ocular conditions. Given the difficulty of the measures, it is possible that this range was partly due to measurement error. However, the fact that we did not see such variation in our other visual measures (e.g., MPOD and CFF were quite normal) and the involved nature of our measurements (we calculated psychometric functions for each participant) suggests that most of the variance is real. We also found that L+Z status, which is a strong correlate of the fast-motion system, appeared unrelated to the slow-motion system. If these results are to be believed, they beg the question: why would one young person be able to see a target moving thirty times slower than another? Hammond & Wooten (2005) showed that CFF in a similar sample of young participants ranged by only a factor of about two, and this study sample was even more homogenous, ranging only by 26%. To the degree that slow motion is significant in real life, this variation matters.

Our preliminary ancillary analyses suggest that slow-motion thresholds may differ between dominant and non-dominant eyes and between males and females. Larger samples could prove useful in disentangling some of these kinds of drivers. Since optical factors did not appear to overly influence our data, other means of measuring slow motion may be possible. For

example, monitor presentations can be automated and may yield faster and more efficient threshold values. Finally, Leibowitz and colleagues (1972) found that correcting peripheral refraction was the key to improving peripheral motion detection. Our participants had acute central refraction but may have differed significantly in peripheral refraction (this may have been a factor driving their large individual differences). Peripheral refraction is rarely rested or corrected in optometric settings. In fact, some refractive corrections may make peripheral refraction worse. For example, toric contact lenses weigh the edge of the lens to ensure proper alignment of the contact with the astigmatic cornea (possibly compromising the refractive characteristics of the edge). Our data, considered with Leibowitz et al. (1972), suggest that correcting peripheral refraction may result in significant visual benefit.

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