

**PARSING PULSES: TESTING THE LIMITS OF
TEMPORAL PHASE PERCEPTION IN HUMAN VISION**

by

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TABLE OF CONTENTS

LIST OF FIGURES.....	v
ABSTRACT.....	vi
Chapter	
1 INTRODUCTION.....	1
1.1 Neural Correlates of Visual Processing Mechanisms.....	3
1.2 Fast and Slow Mechanisms.....	9
1.3 The Temporal Phase Discrimination Task.....	12
2 METHODS.....	20
2.1 Participants.....	20
2.2 Apparatus.....	20
2.3 Stimulus.....	21
2.4 Procedure.....	21
2.5 Analysis.....	26
3 RESULTS.....	27
3.1 Experiment 1 (Binocular).....	27
3.2 Experiment 2 (Dichoptic).....	30
3.3 Within-Subjects Analysis.....	30
4 DISCUSSION.....	34
4.1 Narrowing Down the Bottleneck.....	35
4.2 Levels of Flicker.....	38
4.3 Prior Research, Limitations, and Further Work.....	41
REFERENCES.....	45

LIST OF FIGURES

Figure 1. Visual representation of all eight possible stimulus orientations that were used in Experiments 1 & 2.....	23
Figure 2. Experimental paradigms employed in Experiments 1 (binocular) & Experiment 2 (dichoptic).....	25
Figure 3. Sample results from an individual subject in Experiment 1 compared across four conditions.....	29
Figure 4. Comparison of mean phase discrimination thresholds (μ) in Experiment 1: binocular viewing (x-axis); and Experiment 2: dichoptic viewing (y-axis).....	32
Figure 5. Comparison of within-subjects phase discrimination thresholds (μ) from Experiment 1 (green) to Experiment 2 (yellow).....	33

ABSTRACT

Complete information about temporal visual stimuli is available to human conscious awareness at frequencies below about 10 Hz, a threshold known as the Gestalt Flicker Frequency threshold. At faster frequencies, approximately 10–60 Hz, flicker is perceived but the accurate discrimination of temporal phase is not possible. Above about 60 Hz, the Critical Flicker Fusion frequency, stimuli are completely fused and not perceived as temporally varying. To accurately measure temporal phase limits, care must be taken to avoid activating low-level mechanisms that might invoke a perception of motion, which could bely temporal phase. This study explores the temporal properties and neural mechanisms underlying phase discrimination in human vision by examining the impact of interstimulus spacing and hemifield placement on temporal frequency thresholds in a paired achromatic flicker task. Experiment 1 was conducted with binocular viewing and found that narrow interstimulus spacing resulted in higher phase discrimination thresholds, suggesting contributions from low-level motion detection. Wide spacing relied on high-level processing, which led to reduced thresholds. Experiment 2 utilized dichoptic viewing to assess whether low-level motion detection occurs before binocular combination in V1, with findings showing reduced thresholds irrespective of spacing, suggesting that low-level mechanisms were successfully disabled with dichoptic viewing, and that discriminations were instead performed by high-level mechanisms in higher-

order cortical areas. Despite the wide range of stimuli that jointly activate these mechanisms due to their overlapping temporal ranges, these results reveal that apparent motion and high-level processing appear to work independently. Once apparent motion is eliminated, thresholds drop to 7–10 Hz.

Keywords: temporal phase discrimination; flicker fusion; psychophysics; visual perception; binocular vision; dichoptic vision; apparent motion

Chapter 1

INTRODUCTION

Conscious awareness is experienced as a seamless, unified percept, due in large part to the human visual system's remarkable capacity to operate across multiple simultaneous timescales. This temporal multiplexing is made possible through the collaboration of vision's many specialized subsystems, each of which is tuned to operate within a specific temporal range. For example, early subcortical structures such as the retina and lateral geniculate nucleus (LGN) are known to encode luminance flicker and simple motion at rates exceeding 50 Hz (Hsu et al., 1998; Sincich et al., 2009). In contrast, most higher-order cortical processes appear to plateau at much slower frequencies of approximately 7–10 Hz (Van de Grind, 1973; Aghdaee & Cavanagh, 2007; Holcombe, 2009). This threshold, known as the Gestalt Flicker Frequency (Van de Grind, 1973), marks a perceptual turning point where the discernable on/off sequence of a flashing light gives way to a distinct experience of continuous flicker. However, despite its prominence in everyday perceptual experience, the Gestalt Flicker Frequency (GFF) remains underexamined in the literature.

What makes this limit particularly consequential is the fact that rapid temporal processing appears to be preserved in early stages of the visual hierarchy but is somehow curtailed before reaching the level of conscious awareness. Such a pronounced gap

between the temporal limits of low- and high-level processing could imply the presence of a substantial bottleneck somewhere along the pathway from early vision to conscious awareness — one that likely entails a significant and highly consequential level of information loss. This raises several intriguing questions: If subcortical and early cortical areas preserve high-frequency encoding, what prevents these rapid signals from entering our conscious vision? At what point in the visual hierarchy does vision slow to a maximum of ~10 Hz? Is the observed limit a simple consequence of intrinsic neural constraints, or might it play an important role in preserving perceptual coherence?

In the present study, we attempt to isolate the mechanism that enforces this temporal ceiling. Our aim is twofold: (1) to obtain a precise measurement of the mechanism's temporal limit, and (2) to narrow down its potential neural locus via a process of elimination. Across two experiments, we use a phase discrimination task to measure temporal thresholds while manipulating interstimulus spacing, inter-hemifield placement, and binocular/dichoptic presentation. These manipulations are designed to circumvent faster low-level feature-detection mechanisms (e.g., first-order motion detection), thereby forcing the visual system to rely on slower higher-order mechanisms to perform the task's temporal phase comparisons. By isolating and identifying the processes that impose the Gestalt Flicker Frequency threshold, we seek to better understand how visual subsystems interact at intermediate temporal ranges and to clarify the constraints governing conscious access to high-speed visual information.

Neural Correlates of Visual Processing Mechanisms

In order to discuss temporal processing limits in the human visual system, it is necessary to clearly distinguish between low-level and high-level mechanisms. Low-level mechanisms are generally associated with early visual areas, such as the retina, lateral geniculate nuclei (LGN), and primary visual cortex (V1). These rapid, automatic processes are responsible for detecting basic features like luminance, contrast, color, spatial frequency, orientation, and simple motion (Magnussen, 2000). High-level mechanisms, by contrast, are primarily localized in higher cortical regions along the dorsal and ventral visual pathways, where they integrate basic visual features into complex percepts. These mechanisms involve slower, more complex processes that are essential for tasks like object recognition, spatial awareness, and conscious temporal sequencing (Peirce, 2015; Wurtz & Kandel, 2000). For clarity, the present article will refer to processes localized in the early visual system (i.e., V1 and preceding stages) as “low-level,” while “high-level” processes will be identified as those that primarily operate in cortical regions subsequent to V1.

Temporal information is made available for vision at the earliest retinal level, where temporal properties of external stimuli are encoded during phototransduction via the response timing of retinal photoreceptors (Donner, 2021). Here, temporal limits are imposed by the intrinsic properties of the photoreceptors, including their kinetics, gain, reliability, and the efficiency of signal transduction, as well as the synaptic mechanisms that relay signals to the subsequent processing layer (Field et al., 2018; Schneeweis & Schnapf, 1995; Hsu et al., 1998). These response rates receive further modulation from

circuit mechanisms such as synaptic inhibition (Sinha et al., 2017). In the periphery, cones possessing short axons have been shown to transmit graded luminance signals at rates of up to 50 Hz with little attenuation, whereas rod cells transmit binary signals up to 10 Hz (Hsu et al., 1998). Notably, the 50 Hz response rate found in peripheral cones coincides closely with the generally accepted upper limit on temporal resolution for single-stimulus luminance flicker. Additionally, in studies of non-human primate retinas, rod cells are known to contribute excitatory input to nearby cones (Schneeweis & Schnapf, 1995), while horizontal cells convey inhibitory feedback between adjacent cones, forming antagonistic center-surround patterns that are interpreted by subsequent layers (Sinha et al., 2017; Hsu et al., 1998). Moreover, the excitatory and inhibitory outputs from these lateral interactions form the basis for several feature-detection mechanisms, including directional selectivity, contrast sensitivity, and local motion (Anderson & Vingrys, 2001).

In the next layer of the retina, groups of photoreceptors converge synaptically on individual bipolar cells, which are categorized broadly into two types: ON-bipolar cells, which depolarize in response to light-induced reductions in presynaptic glutamate levels via their metabotropic glutamate receptors, and OFF-bipolar cells, which depolarize in the absence of light due to higher glutamate levels acting on their ionotropic glutamate receptors (Donner, 2021). The initial binding of individual light-detection signals in this layer allows multiple photoreceptor inputs to be integrated with one another, representing their spatial and temporal configuration across longer time windows and broader regions of the visual scene. Accordingly, several key visual mechanisms are either extended or

initiated at this low-level processing stage, including luminance contrast, edge contours, and simple motion. These features are extracted via the concentric spatial arrangement of excitatory and inhibitory bipolar cell outputs, as well as their corresponding temporal relationships (Donner, 2021), before being carried to the next layer for further processing.

At the final retinal stage, multiple bipolar cells synapse upon individual retinal ganglion cells (RGCs) and are modulated by excitatory and inhibitory inputs from bipolar and amacrine cells (Schneeweis & Schnapf, 1995; Brivanlou et al., 1998; Masland, 2017). Retinal ganglion cells appear in a variety of forms, including parasol (M-type) and midget (P-type) ganglion cells, both of which possess receptive fields that exhibit center-surround antagonism and direction-sensitivity (Barlow & Levick, 1965). These properties enhance contrast sensitivity, edge detection, and motion, enriching the spatial and temporal structure of the visual scene (Peirce, 2015; Donner, 2021). However, recent studies have suggested that the majority of RGCs are not individually directionally-selective, but instead that directional selectivity is facilitated through the integration of signals from multiple RGCs (Donner, 2021). Furthermore, outputs from specialized RGCs are organized into separate processing channels—largely according to cell type—which feed into specific layers of the lateral geniculate nucleus (LGN) and superior colliculus (SC). M-type ganglion cells, for example, are transmitted through the magnocellular pathway to the LGN, where they contribute to luminance and motion perception over larger spatial areas. In contrast, P-type ganglion cells transmit color information and fine spatial detail to the LGN via the parvocellular pathway (Field et al., 2018; Croner & Kaplan, 1995; Kaplan & Shapley, 1986). To determine the temporal

response speeds of M-type RGCs, Chichilnisky & Kalmar (2003) used multielectrode recordings of primate retinas to examine their sensitivity to moving bars. The authors determined that directional discrimination accuracy was highest when temporal filtering was done on a time scale of 10-50 ms.

Outputs from the left and right visual hemifields are carried from the retina to the contralateral lateral geniculate bodies. Within the LGN, temporal resolution limits continue to differ between two separate visual channels (Livingstone & Hubel, 1987; Burr et al., 1994; Croner & Kaplan, 1995). These parallel processing channels, which are segregated physically in the LGN's magnocellular and parvocellular layers, enable different types of features to be simultaneously encoded and transmitted to subsequent cortical areas. Of the two pathways, high-frequency temporal processing is generally associated with the magnocellular pathway, due to the shorter latencies, faster decays, and larger receptive field sizes observed in its cells (Livingstone & Hubel, 1987; Schneider et al., 2004). Magnocellular layers specialize in processing low-contrast, achromatic stimuli across larger spatial ranges, and detecting rapid transient changes, including peak responses of 20-30 Hz (Livingstone & Hubel, 1987; DeSimone & Schneider, 2019). This channel serves as the primary input source for cortical regions that process motion and attention (Burr et al., 1994). Parvocellular layers exhibit lower temporal resolution and are more sensitive to sustained stimuli, color, and fine spatial details. Here, peak temporal frequency responses are generally observed at around 10-15 Hz (Derrington & Lennie, 1984; DeSimone & Schneider, 2019). However, Sincich et al. (2009) used micron-scale light flashes to map single-cone inputs to the receptive field

centers of neurons in the macaque LGN, revealing that parvocellular neurons respond reliably to individual cone stimulation. According to these findings, not only are single photoreceptors sufficient to drive downstream neural activity, 30 Hz temporal modulation is preserved in neural signals even at postretinal stages (Sincich et al., 2009; Ratnam et al., 2017). This finding is supported by additional studies that have used psychophysical methods to compare the response sensitivities of retinal ganglion and LGN cells with high-frequency achromatic flicker in the fovea, linking frequency dependence to cones in the retina. (Lee et al., 1996; Donner, 2021) These differential temporal limits exhibited by the LGN's specialized channels increase processing efficiency by allowing multiple aspects of the visual environment to be encoded simultaneously (Livingstone & Hubel, 1987) before being transmitted to the primary visual cortex and superior colliculus.

Upon reaching the primary visual cortex (V1), neural signals from the lateral geniculate nucleus (LGN) enter V1's primary input layers (4a, 4c α , and 4c β), where inputs are segregated by eye and organized into ocular dominance columns, preserving spatial information and binocular disparity (Livingstone & Hubel, 1987). In subsequent layers (2, 3, 4b, 5, and 6), these signals undergo further processing by a number of specialized mechanisms. Inputs from each eye are integrated to produce depth perception and binocular integration, enabling a three-dimensional representation of the visual field. Simple and complex cells in V1 possess receptive fields that are selectively tuned to respond to specific orientations, detect edges, and identify directional motion (Hubel & Wiesel, 1968). Moreover, V1's retinotopic organization uses information inherited from the retina to accurately map spatial relationships across the visual field. Throughout V1,

basic subcortical inputs are processed into detailed representations of the environment, laying the groundwork for higher-order visual processing in later cortical areas (Livingstone & Hubel, 1987). However, whereas temporal properties are preserved from the retina to the LGN, examinations of V1 reveal significantly slower temporal rates and longer integration times, likely due to the complexity of transformations imposed at this stage of visual processing. Hawken et al. (1996) investigated the temporal-frequency selectivity in the primate V1 and LGN in order to study differences in their temporal-frequency tuning. The author's findings indicate significant low-pass filtering between the LGN and the input layers of V1, along with an increase in visual delay of 3 ms. Further low-pass filtering occurs between the input and higher-order layers of V1, resulting in a decrease in high cutoff temporal frequency between the LGN and V1's output layers of about 20 Hz and an increase in visual latency of about 12–14 ms (Hawken et al., 1996). Similarly, Bayram et al. (2016), examined achromatic frequency-response characteristics in the LGN and V1 using fMRI. These authors found a low-pass filtering effect in V1 in the range of 8-12 Hz that was not present in LGN responses.

Beyond the striate cortex, visual information travels along two major pathways: dorsal and ventral, where input from earlier visual areas is further integrated by high-level mechanisms in specialized cortical regions. The dorsal stream, which extends through V2, V3A, V5/MT, and into the parietal cortex, performs functions related to spatial awareness, attention, and complex motion patterns (e.g., object-based motion and trajectory). The ventral stream, which passes through V2, V4, and the inferotemporal cortex, specializes in various forms of object recognition. Areas MT may be of particular

interest, due to its sensitivity to both motion and flicker, as well as its receptive fields, which exhibit tuning for direction and speed. In an fMRI study of apparent motion, Goebel et al. (1998) induced apparent motion using two alternating concentric rings. Areas V1, V3A, and MT all responded to apparent motion, but MT's response was stronger and faster than the other two areas, as well as highly preferential for apparent motion compared to the two flickering controls. Results from this experiment suggest that of any dorsal stream area, MT is the first and fastest at processing apparent motion cues. Apparent motion was also found to activate the inferior and superior parietal lobule (Goebel et al., 1998).

Fast and Slow Mechanisms

The previous section's overview of regions, pathways, mechanisms, and properties provides a number of clues about intermediate flicker thresholds and the mechanisms that create them. Based on temporal rates observed in the early visual pathway, low-level mechanisms appear to detect and process fundamental features of visual stimuli with a high degree of temporal granularity. As these signals feed forward into the higher-level areas of the cortex, however, temporal granularity is diminished as visual processing becomes slower. Donner (2021) offers a plausible explanation for this progressive throttling of high-frequency capabilities, asserting that temporal resolution and integration are inversely correlated, and that losses of temporal acuity scale with the complexity of subsequent integrations. Furthermore, Donner argues that longer integration windows are crucial for certain tasks, either to allow a greater number of input

signals to accumulate over time, or to incorporate input sources across unequal timescales, as is the case in multisensory binding (Fujisaki & Nishida, 2005). Following this line of reasoning, it would be logical to expect high-frequency processes to be concentrated within the early visual regions. Conversely, one could predict a common trend toward slow temporal limits to be shared among higher-order cortical processes, corresponding to the complexity of integrations across multiple sources of input.

Temporal similarities within low-level and high-level vision have been well-evidenced in the literature, and furthermore, tendencies of perceptual and cognitive mechanisms to group together along similar temporal ranges are also observed elsewhere in cognition. This finding that has led authors in several psychological subfields to propose various dual-processing accounts of cognition (for a review, see Evans, 2008). Broadly speaking, dual-process theories separate cognitive processes into two categories, with the first group of mechanisms being characterized as fast, automatic, involuntary, and high-capacity, and the second group described as slow, conscious, deliberate, and capacity-limited (Fodor, 1983; Schneider & Shiffrin, 1977; Evans, 2008).

Of particular interest to the current study is Holcombe's 2009 dual-process account of vision, wherein processes are categorized as "fast" or "slow" based on their temporal resolution. The fast category includes low-level mechanisms such as edge detection (~30 Hz), first-order motion (~30 Hz), and flicker perception (~50 Hz), while slow group includes integrative higher-level mechanisms that facilitate the perception of paired feature types (~4 Hz), acceleration and directional change (~7-10 Hz), and higher-order motion (~8-10 Hz). Holcombe highlights the stark temporal chasm between groups,

noting that every mechanism in the fast category tends to operate above 30 Hz, while in the slow group, no process is faster than 10 Hz. As previously noted, this divide between low-level and high-level mechanisms — with scarcely any visual processes occupying the 10-30 Hz range between the two main groups — strongly implies a rate-limiting information gate that multiple lower-level sources must pass through on their path to the cortex. Further evidence for dual-process grouping comes from Livingstone & Hubel (1987), who devised a series of two-stimulus discrimination tasks and used them to test several feature types. Their faster category is comprised of mechanisms that handle luminance flicker (30 Hz), apparent movement (15 Hz), illusory border/apparent movement (15 Hz), stereopsis (15 Hz), while their slower category contains mechanisms for shape discrimination (5 Hz), orientation discrimination (5 Hz), color alternation (5 Hz), and color flicker (7 Hz). In contrast to Holcombe, however, Livingstone & Hubel propose an alternate origin for their dual-process system, pointing out that movement, stereopsis, luminance contrast, and illusory borders are all features associated with the magnocellular channel, while color and form in the slower group are both associated with the parvocellular channel. Notably, while Livingstone & Hubel report thresholds that diverge from Holcombe's, several thresholds in Livingstone & Hubel's fast category are exactly half of Holcombe's values. This pseudo-alignment likely hints at differences in measurement techniques arising from Livingstone & Hubel's preference for two-stimulus discrimination-based tasks, and thus leaves room for potential agreement between the two accounts.

The Temporal Phase Discrimination Task

Several studies discussed in the previous have measured the limits of temporal perception via psychophysical tasks, often using visual flicker to determine the temporal resolution of a particular task under specific conditions. Temporal resolution, which is defined as the minimum time interval required to perceive two sequential events as separate from each other (Poth et al., 2018), is often measured using Critical Flicker Fusion Frequency (CFFF) tasks (Donner, 2021). This threshold represents the upper limit of basic flicker detection and is generally thought to occur at around 50-90 Hz (Davis et al., 2015). Temporal resolution can also be measured by other means, such two-pulse tasks, wherein brief light pulses must be resolved at short intervals. This task has been used with electrophysiological recordings to evoke and measure neural response characteristics in the retina (30-40 ms), the LGN (50 ms), and in V1 (60-80 ms) (Nilsson, 1979).

Alternatively, temporal phase discrimination tasks can be used to measure the temporal frequency threshold, or critical alternation frequency, beyond which participants are unable to discriminate the relative phase of two or more stimuli (Victor & Conte, 2002; Kanaya et al., 2015). This serves as an index characterizing the temporal granularity of the binding process (Kanaya et al., 2015) and can be used to investigate integration within the same modality or across different modalities, such as visual-auditory bindings (Kanaya et al., 2015; Fujisaki & Nishida, 2005, 2010). Several variations of the temporal phase discrimination task have been developed, including the two-alternative forced-choice (2AFC) employed by the present study. In this version of

the task, participants are asked to perform relative phase judgements of whether temporally oscillating stimulus pairs are in-phase or out-of-phase with one another. Oscillation frequency is randomly modulated throughout the task to determine the maximum temporal frequency threshold where 75% accuracy is achieved by each subject. Rather than measuring temporal resolution directly, this task is used to examine the temporal constraints imposed by the neural integration process that enables comparisons of the paired stimuli, such as judgments of synchrony and asynchrony (Kanaya et al., 2015).

Aghdaee & Cavanagh (2007) used this variation of the task in their investigation of the temporal limits of phase discrimination at different eccentricities and across the four quadrants of the visual field. The authors elected to use a temporal phase discrimination task because their motivation was not to study the temporal limits of flicker directly, but rather to study the temporal limits of attention. In this experiment, Aghdaee and Cavanagh used luminance-modulated achromatic square-wave flicker as their stimulus, which was presented to subjects as pairs of two white discs. Subjects were asked to report whether the stimuli were in-phase or out-of-phase. Two variables were measured in this experiment. The first, eccentricity, was selected in order to discover whether any temporal magnification factor exists. If so, this scaling factor would serve as a counterpart to the spatial magnification factor observed in peripheral vision, which could then be linked with attentive fields. The second factor, interstimulus spacing, can be used to separate first-order motion detectors from high-level processes, thereby leaving only high-level mechanisms to perform the phase discrimination. The upper

frequency limit of this high-level mechanism is designated as the Gestalt Fusion Frequency, a term first coined by Van de Grind et al. (1973). Van de Grind proposed that this flicker fusion threshold occurs between 2-6 Hz, and represents the frequency at which the Gestalt properties of a simple stimulus (e.g., a flickering rectangle, triangle, circle, or cross) achieve temporal persistence. Above this threshold, the individual light and dark phases of an oscillating stimulus can no longer be temporally individuated, as individual images instead fuse into a persistent flicker. Aghdaee and Cavanagh propose that once low-level motion is removed, high-level motion will perform the phase discrimination up to a certain spatial range, and another high-level mechanism will perform the task at higher ranges by judging simultaneity. Either mechanism would individuate the phases of the stimulus, and would thus represent the temporal resolution of attention. Results showed that increasing inter-disc spacing significantly reduces discrimination thresholds, while increasing eccentricity contributes a more moderate reduction. The authors concluded that the reduced threshold of 7-10 Hz represents the operation of high-level mechanisms at the temporal resolution of attention.

Previous studies using 2AFC temporal phase discrimination tasks have consistently demonstrated temporal frequency limits of 15-30 Hz for the discrimination of closely-spaced identical pairs of oscillating stimuli (Aghdaee & Cavanagh, 2007; Forte et al., 1999; Goodbourn & Forte, 2013; Kanaya et al., 2015, Fujisaki & Nishida, 2005). In contrast, temporal limits have been considerably lower (7-10 Hz) when interstimulus separation is widened to distances in excess of D_{\max} (Aghdaee & Cavanagh, 2007; Forte et al. 1999; Victor and Conte 2002), which represents the upper spatial limit for low-level

motion detection and scales with eccentricity (e.g., $D_{\max} = 0.83^\circ$ at 4° eccentricity) (Braddick, 1974; Baker & Braddick, 1985). These results suggest that fast temporal phase discrimination between two closely-spaced visual stimuli is mediated by low-level mechanisms (e.g., first-order motion, edge detection) that detect short-range motion from closely-spaced counterphase stimuli. Conversely, slow temporal phase discrimination across larger spatial distances may rely on higher-level mechanisms, potentially reflecting the temporal resolution of visual attention. Some authors suggest this mechanism may be localized in the right parietal cortex, based on previous findings showing that patients with damage to this area experienced in diminished temporal selection rates in both visual fields (Aghdaee & Cavanagh, 2007; Battelli et al., 2001; Forte et al., 1999; Victor & Conte, 2002; Sigman & Dehaene, 2008).

As exemplified by the experiments discussed above, motion detection is a key factor in most temporal phase discrimination tasks, and is especially relevant when presenting two flickering stimuli. Extensive research has been dedicated to the phenomenon of apparent motion, a phenomenon produced by the spatiotemporal integration of input signals across excitatory and inhibitory sections of neural receptive fields, resulting in the perception of sequentially presented stimuli as a single moving object (Goebel et al., 1998; Lu & Sperling, 2001). Oliver Braddick (1974) used alternating pairs of random-dot patterns to demonstrate that first-order apparent motion occurs only within small spatial displacements. Based on these results, Braddick posited a dual-process system of motion detection, with each process facilitated by distinct neural mechanisms depending on the spatial range of interstimulus segregation: Short-range

motion functions passively and is associated with low-level motion detection. It operates within limited spatial ranges, but is also distributed across the entire visual field, where it is able to respond across multiple parallel instances. Larger spatial displacements are handled by long-range motion, which relies on high-level cortical processing to identify objects and track their movements (Braddick, 1980; Anstis, 1980). Importantly, the author demonstrated the first-order apparent motion effect is not observed when stimuli are presented to different eyes in a dichoptic viewing condition, suggesting that the short-range process operates in the early visual pathway. In a later review, Braddick (1980) posits that the short-range specific-detector process originates from monocularly-driven, directionally-sensitive neurons in the primary visual cortex (V1), as evidenced by the process's limited spatiotemporal range, dichoptic inoperability, and susceptibility to interference from a bright uniform field. The author further suggests the activations of this low-level process are strictly determined by the stimulus and signal the absence of movement (i.e., null motion). In this view, the role of the high-level interpretive process is to arrive at an appropriate "perceptual hypothesis" by selecting from a number of plausible alternatives, while the role of low-level processes is to constrain the available options. Low-level or "fast" mechanisms can be computed within a single receptive field due to their localized processing capabilities. In contrast, slower mechanisms likely necessitate higher-level comparisons, integrating information across broader neural networks. Cavanagh (1992) explored attention in motion perception through two attentive tracking tasks, revealing the existence of an attention-based motion process. In the first task, superimposed luminance and color gratings rotating in opposite directions showed

that even when the luminance grating was masked and not visible, its motion was perceived, while the color grating's motion could only be tracked with attention. The second task demonstrated that the perceived velocity of a color grating increased when attentively tracked, despite typically appearing slow at equiluminance. These findings indicate two independent motion processes: a low-level automatic process that signals motion without attention and an attention-mediated process that provides accurate velocity judgments. Attention's involvement in motion processing is further echoed by Lu and Sperling (2001), who propose a tripartite theory of human visual motion perception consisting of first-order, second-order, and third-order processing systems. The first-order system responds to moving luminance patterns, utilizing motion-energy detectors like Reichardt models, which accurately account for motion direction in a wide range of stimuli. The second-order system processes motion by detecting moving modulations of features such as contrast or texture, invisible to first-order detectors, and involving texture grabbers followed by motion-energy computations. The third-order system computes motion by tracking changes in a salience map, identifying important features and their movement, and is significantly influenced by attention, enabling complex motion perception beyond the capacities of the first two systems.

In the current experiment, we investigated the possibility of an informational bottleneck between slow and fast temporal processing by measuring temporal frequency thresholds for the discrimination of relative phase in achromatic visual flicker. To obtain a precise measurement of the upper limit of the mechanism that defines the ~10 Hz threshold, we aimed to separate high-level and low-level mechanisms that may be active at this

frequency. To this end, we first selected two interstimulus distances — one narrow, and one wide. We predicted higher frequency thresholds in our narrow condition, as participants were expected to benefit from helpful first-order motion cues at higher frequencies. Conversely, we expected these low-level motion percepts to be absent in the wide condition, resulting in lower overall frequency thresholds as subjects were forced to make phase comparisons based solely on higher-order cortical processes. Thus, we began by verifying the difference in temporal thresholds between the two conditions, and the goal of this study was to use targeted experimental manipulations to eliminate it. We also tested within-hemifield and across-hemifield placement (i.e., situating our paired stimuli on the same or opposite sides of the visual field's vertical centerline, respectively) to determine whether low-level mechanisms would be able to detect apparent motion across hemifields. Since early visual areas in the retinas and LGN are known to lack bilateral receptive fields (Schneider et al., 2004), and the right and left visual hemifields are not integrated until V1, we reasoned that any comparison of our across-hemifields stimuli should require interhemispheric integration, which would add additional signal delays and thus may further constrain high-level processes (Battelli et al., 2001). This should be possible after binocular combination in the intermediate layers of V1 or alternatively through interhemispheric transfer via the corpus callosum. Either option would incur a time cost, reducing frequency thresholds. Thus, this manipulation offered to provide potentially valuable clues toward identifying specific neural pathways involved in performing the task, as reduced thresholds in across-hemifield conditions would support localization of low-level motion mechanisms in early visual processing areas, whereas

unchanged thresholds in within-hemifield conditions would suggest the involvement of a high-level process. In Experiment 2, we tested whether dichoptic viewing of stimuli (where each of the two stimuli is only seen by one eye) would elicit low-level motion. We predicted that thresholds would be reduced in the dichoptic condition, regardless of narrow or wide spacing, which would suggest the fast motion mechanism's neural origin is prior to binocular combination layers in V1, and that any temporal thresholds observed in this condition would be strictly attributable to processes facilitated by higher-order cortical areas. In addition to helping localize the neural correlates of low- and high-level mechanisms, this result would also represent a novel method for obtaining the temporal thresholds of slower cortical mechanisms at narrow interstimulus spacings, which would normally be difficult or impossible to measure in isolation due to interference from first-order motion detection.

Chapter 2

METHODS

2.1 Participants

Seventeen subjects volunteered to participate in this study: thirteen in Experiment 1 and fifteen in Experiment 2. Eleven subjects participated in both experiments. Predetermined exclusion criteria required subjects to report phase judgments with a mean accuracy of 75% or higher at the lowest frequency tested (1 Hz) in at least three of the four Spacing + Hemifield configurations. Based on these criteria, data from one subject were excluded from the statistical analysis of Experiment 1 and the within-subjects comparison. Likewise, one subject's data were excluded from analysis in Experiment 2. After exclusions, Experiment 1 totaled twelve subjects, Experiment 2 totaled fourteen subjects, and ten subjects were included in the within-subjects comparison. All subjects were screened for normal or corrected-to-normal visual acuity, gave their written informed consent, and were compensated for their participation.

2.2 Apparatus

A PROPixx projector (VPixx Technologies Inc.) presented grayscale stimuli binocularly at 1440 Hz or dichoptically at 480 Hz. Dichoptic viewing was implemented via a DepthQ circular polarizer attachment (VPixx Technologies Inc.) and passive

circularly polarized 3D glasses. Stimuli were presented frame accurately using MATLAB (The MathWorks, Inc.) and Psychophysics Toolbox 3 functions (Kleiner,) (Brainard, 1997; Pelli, 1997) on a PC running the Ubuntu (version 22.04.3 LTS) operating system.

2.3 Stimulus

Stimuli were a pair of identical monochromatic Gaussians with a standard deviation of 0.3 deg, displayed on a neutral grey background with a central black fixation square. The stimuli were truncated at 3 SD. The luminance values of these stimuli were sinusoidally modulated across time between white and black phases. The spatiotemporal properties of the stimuli were chosen to minimize transient edges or onsets, reduce temporal harmonics, and to preserve the perception of object persistency, in comparison to the white square, square-wave stimuli used in Aghdaee and Cavanagh (2007).

2.4. Procedure

Participants were seated upright in a darkened room at a fixed distance of 62 inches from a 55 × 34 inch wall-mounted projection screen and were required to maintain fixation. Each experimental session began with a three-minute instructional slideshow to ensure task comprehension and allow for visual adaptation to the room's darkened lighting conditions. Following the presentation, subjects completed a brief practice block consisting of 88 trials — one for each stimulus configuration and frequency. During the practice block, subjects received automated feedback in the form of a short beep to

indicate an incorrect response. All participants reported comfort with the task before proceeding to the full experiment. To counteract potential fatigue, short breaks were included at regular intervals (1 per 150 trials). Participants were prompted to temporarily disengage from the task, look away from the screen, stretch, and relax their eyes for ~30–60 seconds before resuming trials.

Participants performed two separate experiments on different days, one in which stimuli were viewed binocularly (both eyes viewed both stimuli), and another in which stimuli were presented dichoptically (each eye viewed a separate stimulus). In each trial, participants fixated centrally and judged whether the stimuli were oscillating in-phase (synchronized with each other), or out-of-phase (alternating such that one turned black as the other turned white). To avoid any offset effects, stimuli oscillated continuously until subjects reported their relative phase judgment with a key press.

In Experiment 1 (binocular), stimuli were varied across eleven oscillation frequencies (1, 4, 7.06, 10, 12.86, 15.65, 18.95, 22.50, 25.71, 27.69, and 30 Hz), two interstimulus distances (1.8° or 5° visual angle, both at 4° eccentricity from the fovea), and two hemifield conditions (across-hemifields, left and right of the vertical meridian; and within-hemifield, above and below the horizontal meridian). Each trial displayed a stimulus pair in one of four Spacing + Hemifield spatial configurations (Narrow + Within, Wide + Within, Narrow + Across, or Wide + Across). Within-hemifield stimuli could appear either to the right or left of the fixation point, and across-hemifield pairs could be located above or below the fixation point, but no temporal threshold differences were found between mirrored variants, so their results were pooled. Each unique

combination of frequency, spacing, and hemifield was repeated 25 times, randomly interleaved among all other conditions, with the relative phase of the two stimuli (in-phase or 180° out-of-phase) randomly chosen for each trial. Experiment 1 sought to accomplish four goals: (1) to replicate Aghdaee & Cavanagh's (2007) findings, (2) to obtain baseline temporal phase discrimination thresholds in a binocular viewing condition to be used in later comparisons, (3) to contrast interstimulus spacing conditions with and without motion cues present, and (4) to test stimulus modifications meant to diminish low-level feature-detection.

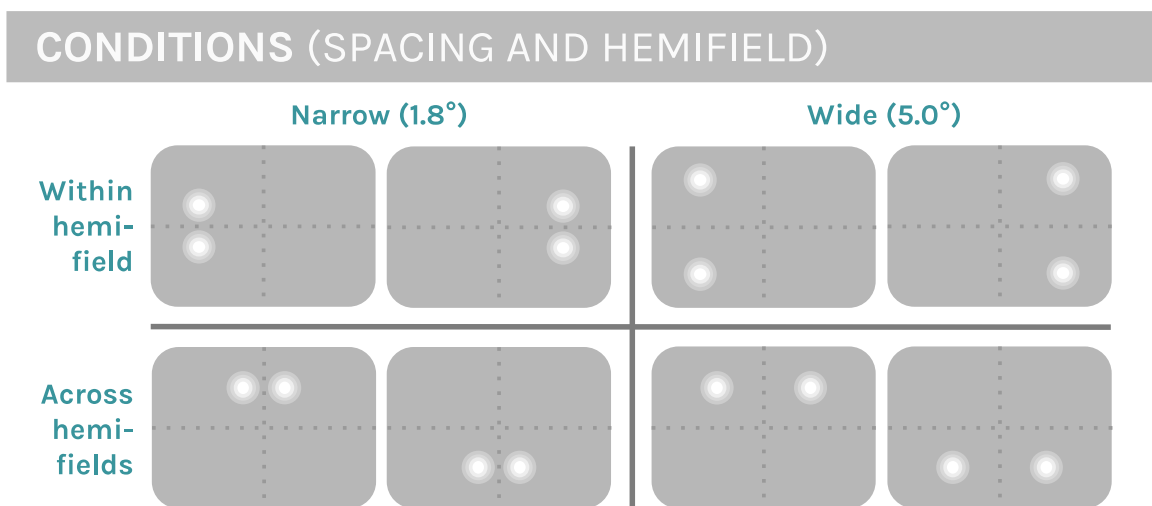


Figure 1. Visual representation of all eight possible stimulus orientations that were used in Experiments 1 & 2. In each trial, the two stimuli either shared a single hemifield (top row) or occupied spaces on either side of the vertical centerline (bottom row). Distance between stimuli was narrowly-spaced (left two columns) or widely-spaced (right two columns). Spacing and Hemifield were combined to produce four unique conditions: Narrow + Within, Wide + Within, Narrow + Across, and Wide + Across. Left/right or upper/lower mirror variants were presented in each of the four conditions (variants shown in each of the four quadrants above). Dotted lines were not present in the experiment.

Experiment 2 (dichoptic) was identical to Experiment 1, save for the following changes: (1) Stimuli were viewed dichoptically, such that each stimulus pair was split, so that one of the two stimuli was visible to only one eye, and the other stimulus was visible only to the other eye. This viewing condition was achieved using a DepthQ circular polarizing shutter (VPixx Technologies) placed in front of the projector lens, switching at 480 Hz. (2) Subjects wore circularly polarized glasses, with each eye polarized in opposite directions, and each stimulus was displayed only on alternate frames so that each eye was presented with only one of the two stimuli. Each eye thus viewed at 240 Hz frame rate, and the oscillation frequencies were adjusted accordingly, resulting in eight frequencies (1, 4, 6.67, 10, 12, 15, 20, and 30 Hz). (3) An exploratory confidence/uncertainty report measure was recorded following each trial but was not analyzed in the present study.

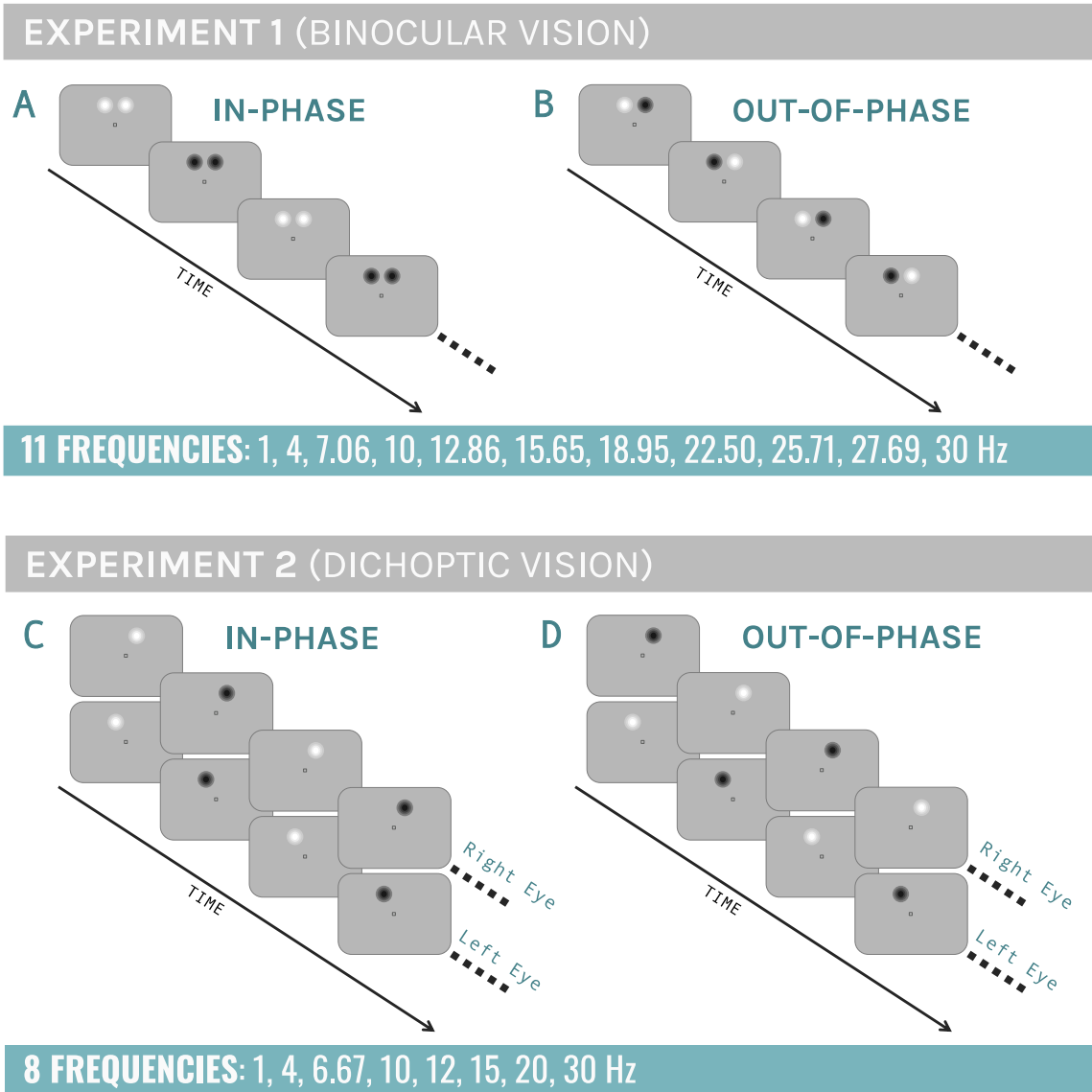


Figure 2. Experimental paradigms employed in Experiments 1 (binocular) & Experiment 2 (dichoptic). In each trial, subjects were asked to discriminate the relative phase of an oscillating stimulus pair and report whether the two stimuli were in-phase (A and C) or out-of-phase (B and D) with one another. Experiment 1 was viewed binocularly, with both stimuli in a pair visible to both eyes (top row), while Experiment 2 also displayed both stimuli simultaneously, but only one stimulus was visible to each eye.

2.5. Analysis

A series of within- and between-subject analyses were conducted to examine how phase discrimination thresholds (μ), slope (σ), and asymptote (a) were influenced by interstimulus spacing, hemifield placement, and viewing method. Experiments 1 and 2 were designed to assess whether phase discrimination is affected by binocular versus dichoptic viewing, as well as how these effects interact with the spatial separation distance of stimuli and their placement within and across visual hemifields. In each experiment, phase discrimination thresholds were obtained for each participant in each of the four Spacing + Hemifield configurations. These thresholds marked the frequency where each subject reported phase judgments with 75% accuracy. The data were fit to the psychometric function $p(\text{"correct"}) = 1 - \left(\frac{1}{2} - a\right) \Phi(f, \mu, \sigma)$, where a is the horizontal asymptote, and Φ is the cumulative normal function, with mean μ and standard deviation σ , over stimulus frequency f . The three parameters were independently subjected to a within-subjects repeated measures ANOVA (Full Factorial Repeated Measures ANOVA Add-In v0.09 for JMP Pro 17.2.0, JMP Statistical Discovery LLC), with viewing condition (binocular or dichoptic), hemifield (same or different) and stimulus distance (near or far) as within-subjects factors.

Chapter 3

RESULTS

3. 1. Experiment 1 (Binocular)

Experiment 1 measured participants' ability to discriminate relative phase when flickering achromatic stimulus pairs were viewed binocularly. Interstimulus distance was varied between narrow and wide, and visual hemifield positioning varied between within-hemifield and across-hemifield conditions. Temporal phase discrimination thresholds for each participant were collected across four conditions (Narrow + Within, Narrow + Across, Wide + Within, and Wide + Across) and 11 oscillation frequencies (1, 4, 7.06, 10, 12.86, 15.65, 18.95, 22.50, 25.71, 27.69, and 30 Hz).

In the narrow spacing conditions, participants achieved mean frequency thresholds (μ) of 12.81 Hz (SEM = 1.29) for within-hemifield and 12.53 Hz (SEM = 1.10) for across-hemifield stimuli. By contrast, wide spacing conditions produced lower thresholds of 9.46 Hz (SEM = 0.57) for within-hemifield stimuli and 8.82 Hz (SEM = 0.49) for across-hemifield stimuli. A two-way repeated measures ANOVA revealed a significant main effect of interstimulus distance on phase discrimination thresholds, $F(1, 9) = 24.81, p < 0.001$. The main effects of hemifield and the interaction between hemifield and distance were not significant, indicating that placing stimuli within the same hemifield or across hemifields did not meaningfully impact thresholds. An analysis

of the asymptote parameter (a) revealed a significant main effect of interstimulus spacing, $F(1, 9) = 10.45$, $p = 0.010$, reflecting the unexpected finding that some subjects were able to discriminate relative phase at above-chance levels in the narrowly-spaced conditions, even at the highest frequencies tested (30 Hz). Pairwise comparisons showed no significant differences between same-hemifield and opposite-hemifield conditions in either of the spacing conditions ($p > 0.05$).

In this experiment, we see a clear divergence between average thresholds for narrow- and wide-spaced stimuli. This difference suggests that motion signals were indeed present in the narrow conditions, which allowed participants use the presence or absence of motion percept to successfully perform distinguish between in-phase and out-of-phase stimuli at higher frequencies, thereby allowing for average phase discrimination thresholds in excess of 10 Hz. By comparison, mean thresholds in both wide-spaced conditions came to rest neatly below 10 Hz, which suggests participants received little to no assistance from motion or other low-level feature cues and instead performed conscious phase comparisons using high-level cognitive mechanisms.

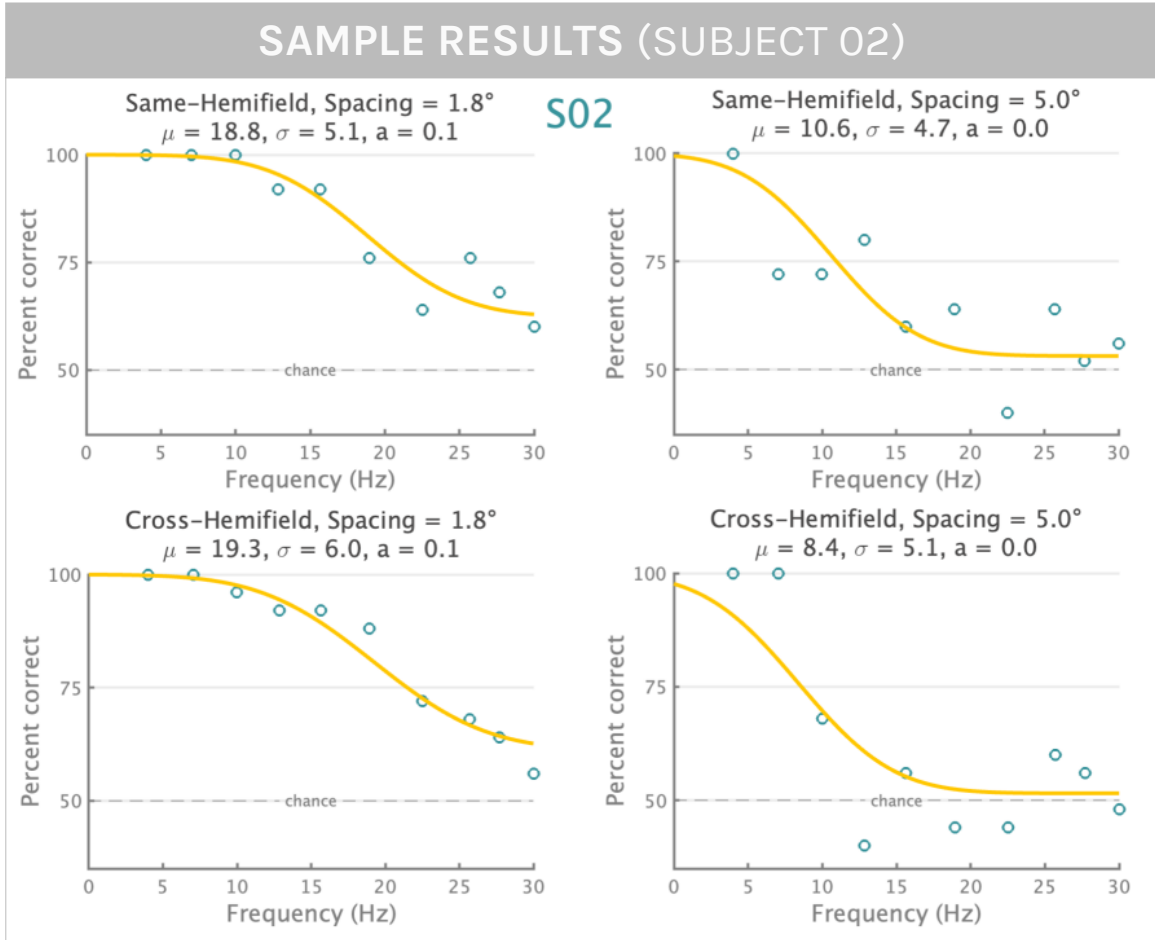


Figure 3. Sample results from an individual subject in Experiment 1 compared across four conditions (clockwise from top left): Narrow + Within-hemifield; Wide + Within-hemifield; Narrow + Across-hemifields; Wide + Across-hemifields. Psychometric functions relate mean accuracy percentages to the oscillation frequency of the stimulus. Phase discrimination thresholds were defined as the frequency at which subject accuracy equals 75%, which is also equal to the mean of the psychometric curve. Chance level performance equals 50%. Here, a significant main effect of asymptote (a) is visible in both Narrow plots (left top and left bottom).

3.2. Experiment 2 (Dichoptic)

In experiment 2, under the dichoptic viewing condition, mean thresholds were observed to be much lower in both narrow conditions, with an average of 10.48 Hz (SEM = 0.70) for the Narrow + Within condition and 9.15 Hz (SEM = 0.91) for the Narrow + Across condition. The difference in thresholds was not so stark for the wide conditions, which were marked at an average of 8.75 Hz (SEM = 0.43) for the Wide + Within condition and 8.56 Hz (SEM = 0.47) for the Wide + Across condition. However, though the gap observed between narrow and wide conditions was certainly less dramatic in the dichoptic experiment as compared to the binocular experiment, a two-way repeated measures ANOVA still revealed a marginally significant main effect of interstimulus distance on phase discrimination thresholds, $F(1, 10) = 5.79, p < 0.05$. This likely implies that although low-level responses may be substantially weakened by viewing the stimuli dichoptically, certain subtle cues may still be present in the Narrow + Within-hemifield condition. Additionally, the asymptote parameter retained a small but significant main effect of spacing $F(1, 10) = 5.77, p < 0.05$, as well as a significant interaction between hemifield and spacing, $F(1, 10) = 9.32, p < 0.05$, reflecting that a few participants were still observed to perform slightly above chance at high frequencies.

3.3 Within-Subjects Analysis

After both experiments were complete, a within-subjects analysis of frequency thresholds (μ) was conducted to examine the effect of our variables across Experiments 1 & 2. This analysis revealed significant main effects of both interstimulus spacing, $F(1,9)$

= 19.50, $p = .0002$ and dichoptic viewing, $F(1,9) = 10.48$, $p = .010$, and a significant interaction between spacing and dichoptic viewing, $F(1,9) = 14.76$, $p = .0040$.

Additionally, a within-subjects analysis of the asymptote parameter revealed significant main effects of both spacing and dichoptic viewing, suggesting that these two factors are at least partially effective methods for curtailing asymptote effects observed in Experiment 1. Based on these findings, we can gather that narrow interstimulus spacing (1.8°) allowed participants to achieve higher phase discrimination thresholds compared to wider spacing (5.0°), consistent with prior research suggesting that closely spaced stimuli may engage low-level motion detection mechanisms that operate at high temporal frequencies (Braddick, 1974; Baker & Braddick, 1985). These low-level mechanisms operate over limited spatial range and cease to function when the distance between stimuli exceeds a critical threshold, necessitating the engagement of higher-level visual mechanisms in order to perform phase comparisons across wider spatial intervals. Although the three-way interaction between experimental viewing condition, hemifield, and distance did not reach statistical significance, $p = .227$, the observed interactions suggest that subtle differences in performance may emerge under certain combinations of spatial and experimental conditions. Further research may be warranted to explore these and other potential interactions in greater depth.

Overall, the within-subjects analysis revealed that stimulus spacing significantly affected phase discrimination thresholds across all three parameters (μ , σ , and asymptote). The interaction between dichoptic viewing and inter-disc spacing was significant for the frequency threshold (μ) parameter, indicating that the impact of

stimulus spacing varies between binocular and dichoptic viewing conditions. Additionally, both dichoptic viewing and inter-disc spacing influenced the asymptote parameter, demonstrating their utility in constraining the availability of low-level perceptual cues during the phase discrimination task.

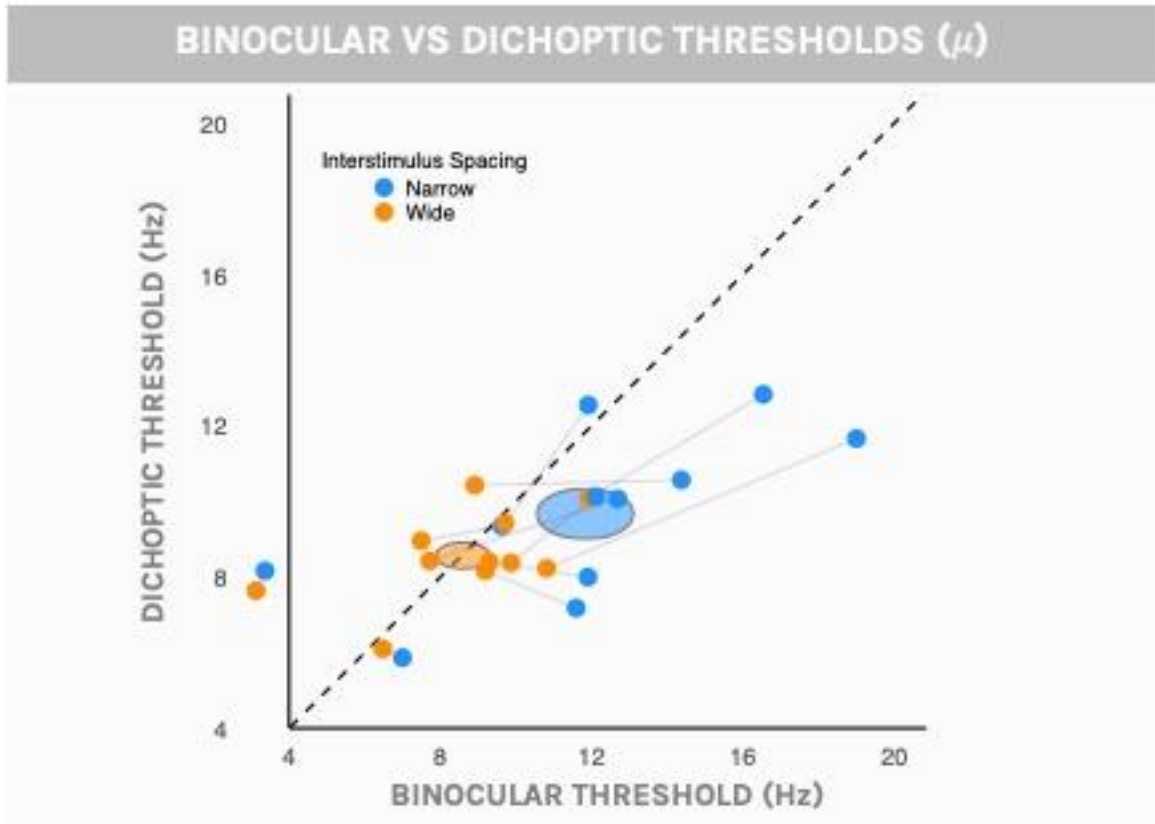


Figure 4. Comparison of mean phase discrimination thresholds (μ) in Experiment 1: binocular viewing (x-axis); and Experiment 2: dichoptic viewing (y-axis). Narrow spacing condition thresholds for individual participants are shown as blue dots, while Wide spacing thresholds are shown as orange dots. Individual participant averages are shown as grey lines connecting Experiment 1 performance to Experiment 2 performance. Blue and orange ellipses represent mean and standard error for each condition, respectively.

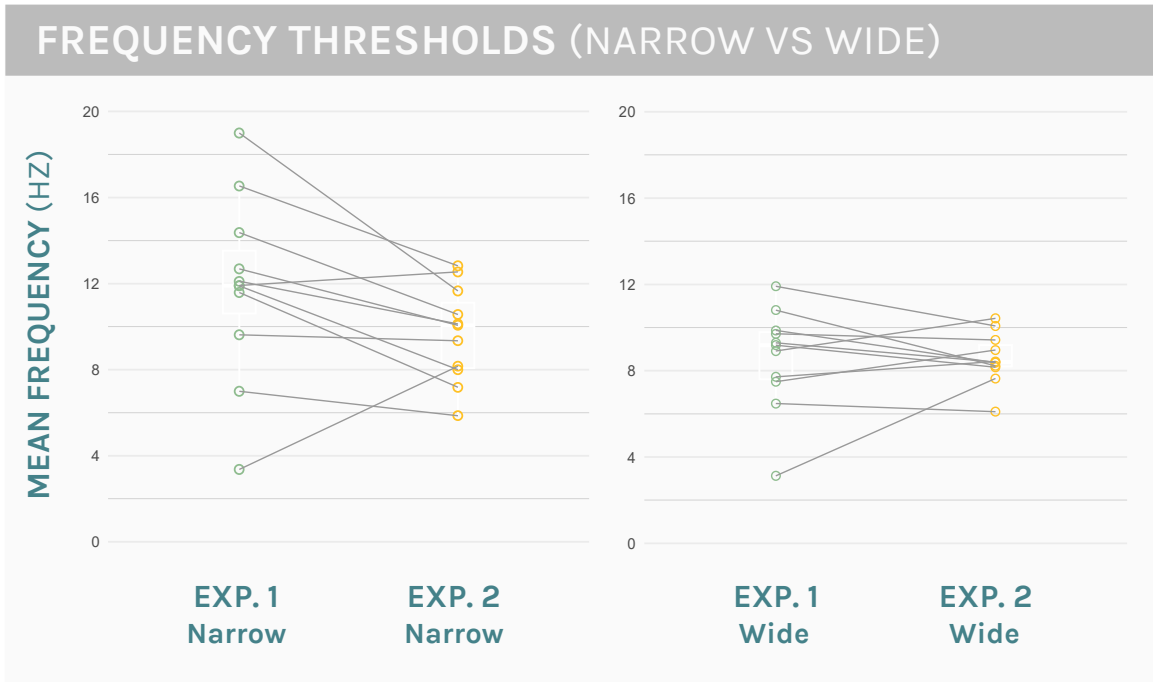


Figure 5. Alternate comparison of within-subjects phase discrimination thresholds (μ) from Experiment 1 (green) to Experiment 2 (yellow). In the left pane, phase discrimination frequency thresholds (μ) are compared between Narrow + Across conditions; and between Wide + Across conditions on the right. Individual participant averages are shown in either green or yellow circles, with grey lines connecting the performance of each subject from Experiment 1 to Experiment 2. Error bars indicate ± 1 SEM.

Chapter 4

DISCUSSION

In two experiments, we examined the limits of high-level temporal processing using a flicker phase discrimination task. Subjects judged the relative phase of achromatic luminance stimuli oscillating at various frequencies, under different spatial and binocular configurations designed to isolate high-level mechanisms while suppressing low-level cues. In the binocular condition, we found that interstimulus spacing significantly affected phase discrimination thresholds. Narrowly spaced stimuli produced higher thresholds, suggesting a contribution from short-range motion detectors. However, hemifield placement had no significant effect. In Experiment 2, we used a dichoptic viewing condition with the intent to further suppress low-level motion signals and disrupt any other early subcortical processes that may be reliant on precise retinotopic matching or interocular synchrony, thereby helping to isolate higher-order temporal mechanisms through a process of elimination. Here too, interstimulus spacing reduced thresholds significantly, but the pattern of results differed, indicating that the dichoptic viewing condition was helpful in reducing low-level contributions and isolating slower integrative mechanisms. A significant interaction found between viewing condition and inter-disc spacing was consistent with our hypothesis that wide spacing and

dichoptic presentation jointly limit the influence of fast, motion-based mechanisms and may assist in narrowing down the temporal boundary of higher-order processes.

4.1 Narrowing Down the Bottleneck

Our comparison between binocular and dichoptic viewing conditions provides important clues about the anatomical locus of the temporal bottleneck. In the binocular condition, early visual areas such as V1 can combine matching inputs from both eyes, allowing for local comparisons within V1's receptive fields to dominate phase discrimination performance, especially when stimuli are narrowly spaced (Braddick, 1974; Baker & Braddick, 1985). However, under dichoptic viewing, the signals from each eye are no longer aligned in time or space in a way that supports early forms of binocular integration. As a result, successful task performance must rely instead on downstream mechanisms capable of comparing asynchronous and spatially disparate inputs, and would likely take place in extrastriate areas or later regions along the visual pathway. Our findings in the dichoptic condition suggest that when early combination fails, a slower, higher-level system attempts to compensate. If that system only operates effectively up to ~10 Hz, as we suspect, then a collapse of performance accuracy above the ~10 Hz threshold offers evidence for a functional boundary where conscious temporal integration begins to break down.

These findings lead us to favor a convergence-based explanation that accounts for the frequency ceiling we observe in the dichoptic condition. When low-level mechanisms are bypassed, and signals from each eye must be brought together without early binocular

integration, performance drops sharply above ~10 Hz. The fact that phase discrimination remains possible at lower frequencies under dichoptic viewing indicates that some form of integration is still occurring, but only within a narrower temporal window. If the higher-order mechanism responsible for comparing those signals is inherently constrained to a narrow band of lower frequencies, then the temporal bottleneck we observe may simply reflect the upper limit of synchrony detection in the absence of fast, feedforward motion cues. In this view, conscious access to relative phase information depends not only on what is preserved by the visual system, but on what can be integrated across asynchronous input channels.

However, our findings may fit well within a dual-process framework of temporal vision, with the first of two dedicated subsystems being a fast, feedforward processing channel specialized for basic feature detection and motion processing at high temporal frequencies, such as tracking rapid changes in luminance or motion, as well as early detection tasks where complex integration may not be a necessity. Notably, these features are also thought to be associated with the magnocellular (M) pathway (Livingstone & Hubel, 1987). M-pathway neurons typically show peak responses around 20–30 Hz (Livingstone & Hubel, 1987; Burr et al., 1994), though evidence suggests they can preserve flicker information up to ~50 Hz at certain stages (Hsu et al., 1998). The second system may align more closely with integrative or attention-based cortical processes, supporting tasks that involve comparison, attention, and conscious access to temporal structure. Unlike the fast subsystem, this one seems to operate within a much narrower bandwidth, plateauing near 8–10 Hz (Aghdaee & Cavanagh, 2007; Holcombe, 2009).

These processes likely rely on broader spatiotemporal integration windows, affording sufficient time for feature binding, attentional allocation, and associative learning (Pöppel, 1997; Donner, 2021). When experimental conditions reduce the availability of fast, low-level signals, as in our dichoptic and widely-spaced trials, observers appear to rely more heavily on the slower subsystem. In these conditions, any temporal constraints on subjects' performance can be reasonably assumed to align with the limits of the slower subsystem's processing capacity. This helps explain why phase discrimination is feasible in some conditions and collapses in others. It also supports the broader idea that visual perception is constructed through the interaction of multiple subsystems, each with its own temporal constraints.

We should note that an information bottleneck need not necessarily reside in any single cortical location, but could instead emerge from the need to synchronizing outputs arriving from multiple channels and sources, each with its own temporal profile. The interaction of feedforward, lateral, and top-down signals further complicates matters, potentially gating or amplifying low-level activity and thereby limiting high-level processes to slower frequencies (Holcombe, 2009; Donner, 2021). However, the stark temporal disparity in temporal resolution between fast and slow system also raises the possibility that a bottleneck could exist between early high-speed operations and later integrative stages. Such a constraint could manifest in two major ways. First, low-pass filtering in cortical areas can restrict high-frequency signals. Even though magnocellular-dominated circuits preserve rapid flicker information (≥ 20 Hz) through the LGN, the primary visual cortex (V1) and subsequent regions often exhibit low-pass characteristics

around 8–12 Hz (Hawken et al., 1996; Bayram et al., 2016). Neurons in V1 must perform more complex computations, such as binocular integration, orientation selectivity, and feature binding, which likely require extended temporal windows that introduce mandatory slowdowns on through traffic. Second, magnocellular-parvocellular interactions could also impose an overall rate limit. The magnocellular pathway alone can handle transient changes at high frequencies (~20–30 Hz). However, meaningful object-based perception often depends on integration with the parvocellular (P) pathway, which operates more slowly (~10–15 Hz) (Livingstone & Hubel, 1987). When signals from both pathways converge in higher cortical areas, the slower channel effectively sets the pace for conscious access.

4.2 Levels of Flicker

Within the 0 to 50-60 Hz range, flicker detection is consciously perceived, and is somewhat enhanced in the peripheral visual field. Even at high frequencies in the experimental task where phase discrimination was no longer feasible, flicker remained clearly visible. Temporal resolution varies across the visual field, with a spatial distribution resembling the retinotopic distribution of rods and cones. This suggests a feedforward channel, most likely the retino-thalamo-cortical pathway, where output from photoreceptors has been shown to reach conscious awareness with minimal loss of temporal resolution. The primary candidates for this mechanism include peripheral cone photoreceptors and the magnocellular pathway of the LGN.

In the 15-30 Hz range, flicker is visible and motion are perceptually dominant,

and relative phase is not consciously discriminable. However, most participants reported being able to perform the task solely via cues offered by short-range motion detection. Apparent motion was evoked only by counter-phase stimuli, creating an illusion commonly described as having the appearance of “one flickering object moving back and forth” (i.e., exhibiting strong and alternating directionality), which implies a capacity for orientation selectivity in the mechanism responsible. In-phase stimulus pairs did not elicit a motion percept and invariably appeared as two separate objects. Thus, because first-order motion was present in one phase type and not the other, subjects were able to determine relative phase in >10 Hz trials based on a simple yes/no check for the presence of motion. First-order motion detection is known to have a spatially limited range of operation, losing operability at wide interstimulus distances that exceed D_{\max} (i.e., the spatial limit of motion detection) (Baker & Braddick, 1985). In the present study, motion detection was successfully subverted in widely spaced conditions, wherein stimulus pairs were separated at 4° of visual angle. LGN, V1, with the spatial limit corresponding well to receptive field sizes in V1, possibly related to the magnocellular and/or dorsal pathways.

In the 0 to 7-12 Hz range, high-level integration mechanisms allow for conscious phase comparison. These mechanisms exhibit low temporal resolution but operate at high spatial resolution, too wide for local phase binding between receptive fields, and lack a strong motion percept. Judgments in this range are based on detecting synchrony in in-phase stimuli, requiring real-time comparison of stimulus pairs. The stimuli must match in attribute (e.g., achromatic-achromatic), or else thresholds drop to the 3-5 Hz thresholds

found in inter-attribute and inter-modal discrimination tasks. Potential candidates for these high-level mechanisms include cortical binding processes and the temporal resolution of attention, potentially localized in dorsal areas involved in attention, such as the parietal cortex.

A phase discrimination task was used by Kanaya et al. (2015) to measure the limits of temporal integration in audition, while varying the interstimulus spacing of auditory tones. The authors obtained frequency thresholds of 14-16 Hz in closely-spaced and 7 Hz in widely-spaced auditory stimuli, similar to results reported in vision. The authors conclude that similar temporal binding mechanisms may operate over same-type stimuli, regardless of overall modality. However, a higher threshold of 18 Hz found using a dichotic listening condition suggests that some interaural integration mechanisms work differently than binocular combination in vision. Even slower temporal limits have been reported in phase discrimination tasks using paired stimuli of different types. Fujisaki & Nishida (2005) asked subjects to discriminate the synchrony or asynchrony of luminance-modulated gaussian flicker and amplitude-modulated white noise. Results suggested that relative phase judgments of audio-visual pairings are only possible at frequency rates of 4 Hz or lower. Results from auditory within-modal discrimination tasks and cross-modal discrimination tasks may be only tangentially related to the low-level mechanisms involved in flicker discrimination, but might provide useful clues about high-level processes. If, for example, a slow, high-level attentional process is responsible for binding same-attribute within-modal inputs in vision, and a nearly identical process exists in audition, certain findings may be generalizable.

4.3 Prior Research, Limitations, and Further Work

Our findings are also consistent with previous research by Aghdaee and Cavanagh (2007), who showed that increased inter-disc spacing reduces the contribution of low-level motion detection in phase discrimination tasks. Furthermore, the thresholds we collected tend to align closely with Holcombe (2009)'s dual-system theory, which posits the existence of fast, low-level mechanisms for detecting rapid changes and slower, high-level mechanisms for more complex temporal tasks. By extending the experimental design to include cross-hemifield and dichoptic viewing conditions, we provide additional evidence that high-level temporal mechanisms can be isolated and studied independently of low-level cues. Additionally, our observations suggest alignment with accounts of discrete sampling, wherein cortical oscillations in the alpha and theta bands periodically refresh visual representations at rates that closely resemble the upper-bound frequencies evident in conscious vision (VanRullen, 2016). By implication, any inputs arriving above this sampling rate would risk going undetected or being merged into a unified percept, effectively limiting the system's capacity to register high-frequency phase offsets or rapid transitions. Thus, while low-level circuits might transiently detect faster flicker, the global awareness of such signals appears to hinge on integration intervals limited to around 10 Hz or lower.

The results of our study have several important implications. First, they support the notion that temporal perception is mediated by a dual-system process, with distinct mechanisms for handling rapid and slow visual changes. This understanding can inform future research into the neurophysiological mechanisms which facilitate temporal

perception. Second, our findings highlight the effectiveness of using dichoptic presentation with increased interstimulus spacing to isolate high-level temporal mechanisms. The methodological approach employed in the present study, particularly the joint manipulation of interstimulus spacing and binocular/dichoptic viewing conditions, represents a useful framework for isolating and studying high-level temporal mechanisms.

While the present study offers new insight into the temporal limits of high-level visual mechanisms, several limitations should be noted. One concern involves the potential for cognitive fatigue, given the duration of the experimental sessions. This is a known drawback of the method of constant stimuli, particularly when task difficulty increases at higher flicker rates. Although our participants remained compliant and engaged, future work may benefit from distributing sessions across multiple days or incorporating more frequent breaks to mitigate fatigue-related effects.

Additionally, it is worth noting that some subjects in the present study reported that first-order motion was diminished or altogether eliminated during dichoptic viewing of cross-hemifield pairs, even in narrowly spaced dichoptic viewing conditions. This particular interaction would have been highly desirable to observe in our study, but it was not found to be statistically significant in the between-subjects analysis. However, further investigation with adjusted conditions could potentially be warranted, as a positive finding might suggest that dichoptic viewing impeded the involvement of cortical regions located beyond the point of binocular recombination (e.g., Area MT) in facilitating first-order motion.

Incorporating eye-tracking technology could help to control for confounding eye movements and also help to analyze the role of eye movements in phase discrimination tasks. It is possible that microsaccades and other subtle shifts in fixation may interact with spatiotemporal integration windows, especially when stimuli are presented near perceptual thresholds. By precisely measuring eye movements over the course of phase discrimination task, we could gain additional insight into whether observed limits on phase discrimination reflect intrinsic neural constraints or are partially driven by micro-saccadic dynamics and fixation instability. In this way, eye-tracking could serve a dual purpose as a control variable and a key investigatory tool.

Finally, further work should be dedicated to exploring Livingstone & Hubel's 1987 proposal that the magnocellular and parvocellular pathways could themselves serve as distinct channels for carrying fast and slow visual information. Since these pathways are known to carry transient and sustained signals along separate temporal bandwidths, and since the channels remain segregated throughout the LGN and V1, they could very easily represent a structural basis for the separation of fast and slow processes into a dual-process system, as has been suggested. If Livingstone & Hubel are correct, their view holds the potential to dramatically redirect our pursuit of the temporal bottleneck. Instead of a late-stage rate-limiting mechanism, we may need to consider that the temporal bottleneck could be baked into the visual system's architecture from the outset. Fortunately, Livingstone & Hubel generously offer two methods with which to selectively disable magnocellular processing: equiluminance and voluntary fixation. If one can experimentally suppress the fast channel and observe corresponding shifts in

perceptual thresholds, this may reveal further clues about the source of the ~10 Hz limit on conscious awareness.

In conclusion, our findings emphasize the distinct roles of high- and low-level mechanisms in processing temporal information and highlight the importance of targeted experimental designs in studying complex perceptual processes. This research set out to distinguish between the individual roles and contributions of fast and slow temporal subsystems in conscious visual awareness, focusing on the critical range where conscious perception shifts from temporally flexible to rate-limited. Understanding how individual visual processes respond to stimuli at different spacing distances and in novel viewing conditions reveals broader implications for models of visual processing, offering further insight on how attention, feature-binding, and interhemifield integration collectively define the upper bound of conscious temporal resolution.

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