University of Nevada, Reno

Quantification of a Novel Illusion: Flicker-Induced Induced Motion

A thesis submitted in partial fulfillment
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by

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We recommend that the thesis
prepared under our supervision by

Sion Gutentag

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Tamara Valentine, Ph. D., Director, **Honors Program**

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Abstract

Visual illusions are often studied and analyzed to better understand the neural basis of perception. This project aims to quantify flicker-induced induced motion (FLIIM), a newly discovered form of induced motion that causes a stationary object to appear to move when displayed with other moving objects *only* when all of the objects are flickering. The results revealed that the flicker rate at which FLIIM is the strongest is 2 Hz and that FLIIM gets weaker as the flicker rate increases. The results also revealed that FLIIM is strongest in parafoveal vision and gets weaker in foveal vision. Finally, using isoluminant stimuli, it was determined that FLIIM occurs in second-order motion perception. These findings help refine future models of motion perception and other models that utilize flickering stimuli.

Acknowledgements

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Introduction

Motion perception is the neural summation of visual stimuli to determine the speed and direction of objects relative to the surrounding environment. Motion perception is comprised of two parts: first-order motion perception, which involves detection of variation in luminance (brightness) across the retina, and second-order motion perception, which involves detection of variations in contrast or color across the retina (Lu & Sperling, 2001). Motion receptors are neurons that respond directly to motion across receptive fields that function by correlating their individual responses to a moving stimulus (van Santen & Sperling, 1985). Because motion detectors' receptive fields tend to be very small (extending ~1º- 4º of visual angle), the perception of a moving object relies on pooled information across the receptive fields of many neurons. This 'global' processing is readily observed in the phenomenon of 'induced motion'.

Induced motion is the perceived illusory motion of a stationary object due to the movement of other objects within the visual field (Duncker, 1938). A famous example of induced motion can be experienced when viewing the moon on a cloudy night. Assuming the clouds are moving in one direction due to the wind, the moon appears to be moving in the opposite direction when the moon would appear stationary.

Flicker-induced induced motion (or FLIIM) is a newly discovered form of induced motion that occurs when a stationary object appears to move when displayed with other moving objects *only* when all of the objects are flickering. Because visual illusions are often used to study how the brain works, determining how FLIIM occurs can reveal how perceptions of the world are created. This project aims to quantify the parameters within which this newly discovered form of induced motion occurs.

The quantification of FLIIM involves three steps. The first step determines at which flicker rates FLIIM occurs, thereby identifying the temporal tuning characteristics of neurons underlying FLIIM. The second step in this project determines whether FLIIM is equally strong across the visual field because the distribution of different neural populations is heterogeneous across the visual field. Determining which portions of the visual field undergo FLIIM hints at the populations of cells within which FLIIM occurs. The final step of the project determines if FLIIM exists for second-order motion perception by attempting to create the effect using isoluminant color stimuli. While induced motion is not generally color dependent (Day & Dickinson, 1977), determining whether FLIIM occurs in the pathways responsible for second-order motion further narrows the populations of cells in the visual pathway in which FLIIM occurs.

The quality of flicker involves rapid alternation in brightness or other properties of an image. While flicker has not been explored in the context of induced motion, flickering stimuli are utilized in many models to investigate diverse topics in neuroscience. The combination of the three experiments performed in this project will identify how flicker can create induced motion. The results of this project will refine future models of motion perception as well as other models that utilize flickering stimuli.

Literature Review

Flicker-induced induced motion (FLIIM) is a form of induced motion in which a stationary object appears to move when displayed with other moving objects *only* when all of the objects are flickering. FLIIM is a newly discovered form of induced motion built on earlier research of classical induced motion, induced motion illusions, and the various forms of vision in which induced motion is known to occur. This literature review will provide an overview of these studies to present the roots of induced motion research that FLIIM builds upon. Theories that seek to explain why induced motion occurs follow from the overview of these studies. Also necessary is a discussion of the neural correlate of induced motion. After this extensive discussion of induced motion, an overview of how flicker independently interacts with the visual system will be presented. Discussing induced motion and flicker together will create a background for flicker-induced induced motion experiments

Induced Motion

The documentation of induced motion can be traced back to Ptolemy (100-170 A.D.), who noted in *Optics* that an unmoving object could appear to move if its surroundings were moving (Smith, 1996). In 1929, induced motion was classically defined in a laboratory setting by Karl Duncker, who showed that a stationary circle of light enclosed in an oscillating, moving frame appeared to move in the opposite direction of the frame (Duncker, 1938). It was also found that if the circle moved, it appeared to move slower when the frame was moving in the same direction but faster when the frame was moving in the opposite direction. This illusory motion is known as the Duncker illusion.

A modified version of the Duncker illusion, in which a centralized red circle moved horizontally while a background of black dots moved vertically, illustrates that motion can be induced in directions other than those in which the fixation target is moving (Zivotofsky, 2004). In this illusion, as the background circles moved upwards, the centralized red circle appears to move diagonally and upward from its true horizontal path. Peak effects of this modified illusion occur at 20° to 40° of angular separation between the test dot and background's movements, which is consistent with other directional illusions (Farrell-Whelan, Wenderoth, & Wiese, 2012). This modified experiment further expands upon the effects that a moving background can have on a stationary target.

While classical induced motion illusions explored the frontoparallel plane, or motion across the field of vision, induced motion also occurs in the depth dimension. With monocular viewing, a stationary target that is surrounded by a frame moving in the depth dimension appears to move in the depth dimension (Farnè, 1972). However, in an experiment that displayed a separate target to each eye, one moving and one stationary, no significant induced motion was observed in the stationary target (Ittelson, 1951). While motion cannot be induced between eyes, motion in the depth dimension can be induced monocularly when apparent size change is the cue to motion.

Illusory motion in the depth dimension can also be induced using binocular disparity as a cue. In one study, the magnitude of induced motion was compared between binocularly viewed lateral and depth motion (Harris & German, 2008). In the lateral motion condition, angular motions for each eye were the same while, in the depth motion condition, angular motions for each eye were opposite. The magnitudes of difference between the two conditions were not significant, suggesting that the mechanism and possibly underlying circuitry for induced motion in the frontoparallel and depth planes are the same.

Induced motion, first investigated using the Duncker illusion, can occur in any direction in both the frontoparallel and depth planes. While it is important to understand all of the ways in which induced motion occurs, it is more useful to understand why induced motion happens in order to learn more about the human brain.

Cause of Induced Motion

It has been found that motion can be induced regardless of whether the participant fixates on the stationary target or the moving inducer (Gogel & Griffin, 1982; Likova & Tyler, 2003). These findings lead to the theory that the Duncker illusion may be explained by the image of the stationary target moving across the retina as the participant's eye tracks the moving frame. While the classical Duncker illusion paradigm required the participants to fixate on a stationary target, participants may have inadvertently tracked the movement of the background frame. However, several eye tracking experiments have found that eye movement was not responsible for the induced motion effects experienced in the Duncker illusion (Bassili & Farber, 1977; Brosgole, Cristal, & Carpenter, 1968; Zivotofsky 2004). These experiments compared the degrees of visual angle that the frame moved across the visual field with the degrees of visual angle the eye moved. The results of these experiments indicated that induced motion effects were present while the eye moved significantly less than the inducing frame moved (as measured in degrees of visual angle). These findings suggest that the induced motion effect occurs within vision processing areas of the brain rather than on the retina.

Another proposed theory suggests that induced motion is a resolution of ambiguity (Day, 1978). In a display that contains one moving object and one unmoving object, it is perceptually difficult to determine which object in the visual field is moving without a stationary reference such as a background or frame. In the natural world, motion perception is experienced as the speed and direction of objects relative to their environments. Without a reference such as the environment, illusory motion is experienced. This theory can be demonstrated in the laboratory: if a stationary frame is placed around an illusion such as the Duncker Illusion, induced motion effects are measurably lessened. More recently, research has shifted away from how induced motion happens and toward where it happens in the brain.

hMT+, The Neural Correlate of Induced Motion

The human cortical area hMT+ has been implicated as the neural correlate for induced motion (Takemura, Ashida, Amano, Kitaoka, & Murakami, 2012). Measured using functional magnetic resonance imaging, hMT+ was active during a classical Duncker illusion when a central target appeared to move opposite of the background. Importantly, hMT+ was inactive when the central target moved with the background, indicating that hMT+ activity is related to induced motion rather than actual object speed.

Human cortical area hMT+ is a subsection of the medial temporal visual area (often called MT or V5), which contains a high number of direction selective neurons. This area is active in the perception of motion and is especially active when opposing motions are detected (Born & Bradley, 2005; Moutsiana et al., 2011). First- and second-order motion converge and are processed in hMT+ (Smith, Greenlee, Singh, Kraemer, & Hennig, 1998). In summary, hMT+ can be considered a primary processing center for motion perception and induced motion.

Flicker on the Visual System

Though it has not been investigated in the context of induced motion, the quality of flicker is closely linked to motion perception. One way this link is apparent is in the finding that motion-direction detection training can raise the maximum flicker that can be perceived (Thompson & Stone, 1997). The upper limit of detectable flicker is what is known as the flicker-fusion threshold, or the flicker fusion rate[1] (Landis, 1954). Under normal conditions, the limit for detecting flicker (approximately 60 Hz for light flickering stimuli) is much higher than the limit for consciously discriminating stimulus luminance oscillations (Battelli, Pascual-Leone, & Cavanagh, 2007; van de Grind, 1997). The ability to raise this flicker fusion threshold with motion-direction detection training demonstrates a close association between the detection of flicker and motion. Furthermore, flickering motion illusions are often utilized to study motion perception, hinting that the quality of flicker in a stimulus bestows a perceptual property of motion.

Beyond flicker's link to motion perception, flickering light has been shown to have numerous extreme effects on the visual system. Flickering light has been known to induce visual hallucinations, with differing flicker frequencies causing different complexities of hallucinations (Allefeld, Pütz, Kastner, & Wackermann, 2011; Becker and Elliott, 2006). Flickering images can also cause visually induced motion sickness (VIMS), the severity of which can be dependent on flicker frequency, peaking between 0.2 and 0.4 Hz with minimal severity at higher and lower frequencies (Diels & Howarth, 2013). While the effects of flicker on the visual system have been measured and recorded, the mechanisms that underlie these effects are not well understood.

Anatomically, flickering stimuli are processed later than (or upstream of) static stimuli (Nishida & Sato, 1995). In an experiment that compared motion aftereffects[2] of

[1] Flicker-fusion threshold/Flicker fusion rate: defined as the frequency at which an average viewer can no longer detect flicker 50% of the time.
[2] Motion aftereffects: The perceptions of movement in stationary objects after focusing on a moving visual stimulus.

static and flickering images, it was found that flickering stimuli are affected by second order motion more than static stimuli, indicating a higher level of processing. This indicates that flickering stimuli take more processing than static stimuli to be perceptually understood.

Induced motion is a well-defined perceptual phenomenon, and flickering stimuli have extensive and varied effects on the visual system. However, no research has been done linking flicker with induced motion prior to this project, and what we call flicker-induced induced motion has not previously been discovered nor defined prior to this project. This project quantifies the parameters in which FLIIM occurs by investigating the temporal tuning characteristics of FLIIM, where it occurs in the visual field, and whether it occurs in both first and second-order motion perception.

Materials and Methods

This quantification of flicker-induced induced motion performed in this project involved three experiments. The first experiment was designed to determine at which flicker rates FLIIM occurs, thereby identifying the temporal tuning characteristics of neurons underlying FLIIM. The second experiment in this project determined how FLIIM varies across the visual field, narrowing the populations of cells in which the effect occurs. The third and final experiment confirmed whether or not FLIIM occurs in second-order motion perception, again narrowing the populations of cells in which the effect occurs.

Participants

Ten observers participated in experiment one (six male, four female), nine in experiment two (six male, three female), and nine in experiment three (seven male, two female). All participants were undergraduate or graduate students of the University of Nevada, Reno, and had normal or corrected-to-normal vision. Participants provided written informed consent.

Apparatus and Display

The computer used to generate the stimulus was a 2.5 GHz Mac Mini with an Intel HD Graphics 4000 graphics processor and 768 megabytes of DDR3 VRAM. Stimuli were programmed and presented using the Psychophysics Toolbox (Brainard, 1997) for MATLAB (Mathworks Inc., Natick, MA). Stimuli were displayed on a Dell Trinitron CRT monitor (60 Hz refresh rate). Participant view distance from the screen was 74 cm.

Experiment 1

In order to determine the flicker rates at which FLIIM occurs, on a grey background four 140-pixel diameter circles were presented on screen for 1000 milliseconds per trial. Each circle was located in a quadrant 150 pixels from the center of the screen. During all trials, participants were asked to fixate on a small black dot located in the center of the screen. In each trial, one circle was randomly selected to remain stationary, while the other three moved in random directions at a rate of 1 pixel per frame. (See Figure 1)

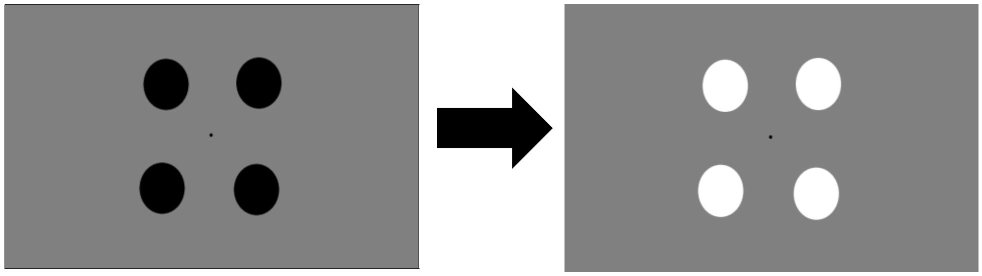

Figure 1. Example of Two Consecutive Frames of Experiment 1. Between frames, the circles have changed from black to white, and three of the circles have moved by 1 pixel in a random direction. In the next frame, the circles change back to black, creating a flicker effect, and the three moving circles again shift 1 pixel in a random direction.

In control trials, the circles did not flicker, instead remaining a constant black or white. In experimental trials, the circles rapidly alternated between black and white in unison, creating a flicker effect at rates of 2 Hz, 4 Hz, 6 Hz, 7 Hz, 8 Hz, 9 Hz, 10 Hz, 12 Hz, or 14 Hz. After each trial, each quadrant was numbered (“1”, “2”, “3”, or “4”), each participant was prompted to determine in which numbered quadrant the stationary circle was located. After the participant entered a decision with the keyboard, the next 1000 millisecond trial began.

Each participant was presented with five practice trials, followed by 200 experimental trials at 20 trials per flicker rate. Only one flicker rate was tested per trial. Experimental trial conditions were randomly distributed.

For analysis, each of the participants’ responses were recorded as either correct (if the participant correctly selected the quadrant in which the stationary circle was located) or incorrect (if the participant selected any of the other circles). Because flicker-induced induced motion causes a stationary object to appear to move, and the task requires the participant to determine which circle was stationary, reduced accuracy in the task indicates the presence of FLIIM. Knowing this, it is possible to anticipate what the results of this experiment may look like. If the stimuli are not flickering, and the participant is easily able to select the circle that is stationary, then participant accuracy will be at or near 100% (Figure 2). Conversely, if the stationary circle is extremely difficult to discern and the participant randomly selected a response, participant accuracy would be at or near 25% (Figure 3).

In this experiment, as the stimuli are flickering and FLIIM makes the stationary circle difficult to discern, participant accuracy decreases. If FLIIM increases as the flicker rate increases, participant accuracy will decrease as the flicker rate increases (Figure 4). However, if FLIIM is strongest at some specific intermediate flicker rate, then participant accuracy will gradually decrease until the "optimal" flicker rate, after which accuracy will gradually increase again (Figure 5).

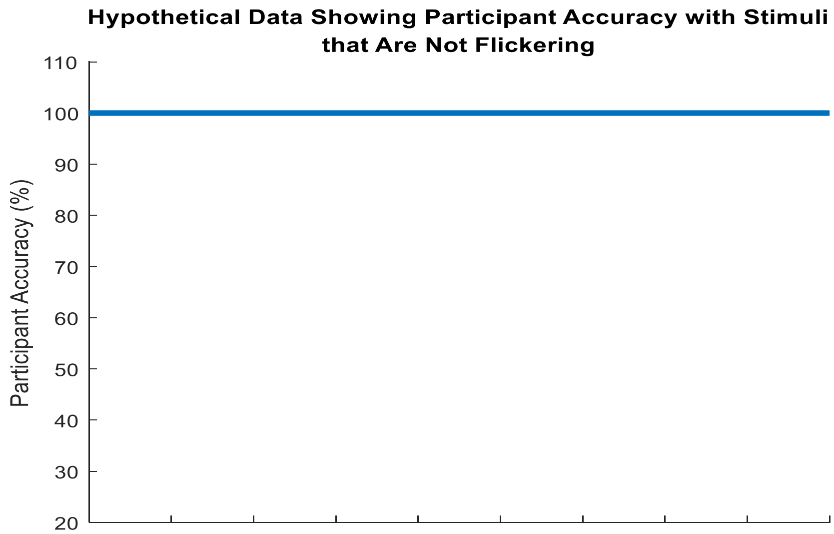

Figure 2. Hypothetical Data Showing Participant Accuracy with Stimuli that Are Not Flickering. Because the stimuli are not flickering, the participant is easily able to select the circle that is stationary and participant accuracy is very high, at or near 100%.

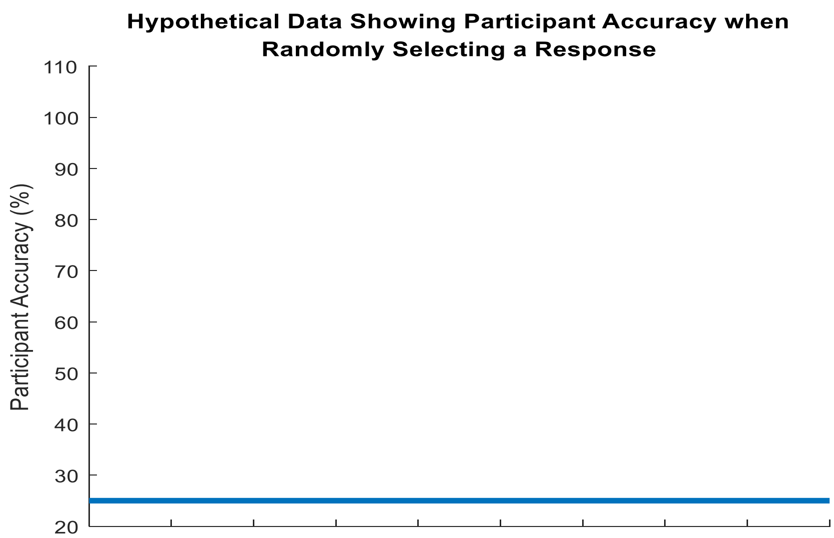

Figure 3. Hypothetical Data Showing Participant Accuracy when Randomly Selecting a Response. If selecting the stationary circle is exceedingly difficult and participants make a random selection, participant accuracy will be at or near 25%.

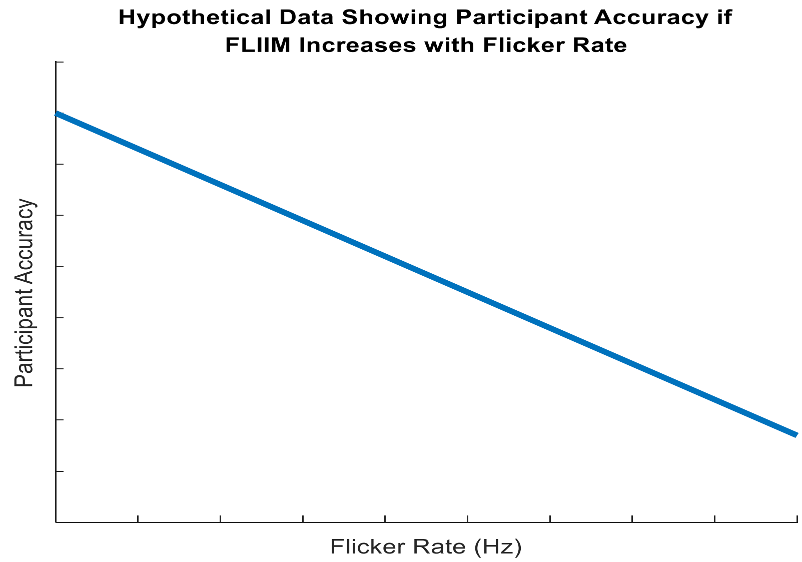

Figure 4. Hypothetical Data Showing Participant Accuracy if FLIIM Increases with Flicker Rate. Because flicker-induced induced motion causes a stationary object to appear to move, and the task requires the participant to determine which circle was stationary, reduced accuracy in the task indicates the presence of FLIIM. Therefore, if FLIIM increases as flicker rate increases, participant accuracy will decrease as flicker rate increases.

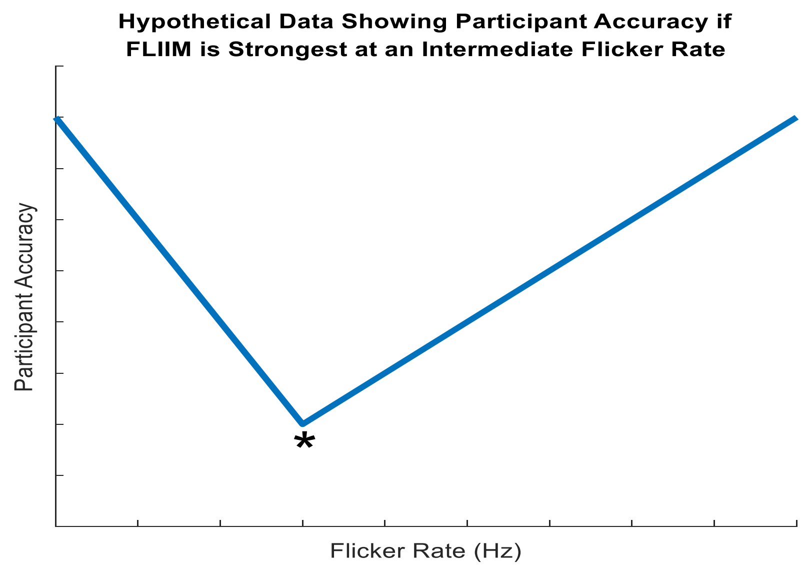

Figure 5. Hypothetical Data Showing Participant Accuracy if FLIIM is Strongest at an Intermediate Flicker Rate. If FLIIM is strongest at some specific intermediate flicker rate, participant accuracy will gradually decrease until the “optimal” flicker rate (marked with a star), after which accuracy will gradually increase again.

Experiment 2

In order to determine how FLIIM varied across the visual field, the stimulus used in the second experiment was identical to the first experiment, except the starting positions of the circles were modified from 150 pixels from the center of the screen to 100 pixels from the center of the screen (Figure 6). Other control trial parameters, experimental trial parameters, and flicker rate conditions were the same as in experiment one.

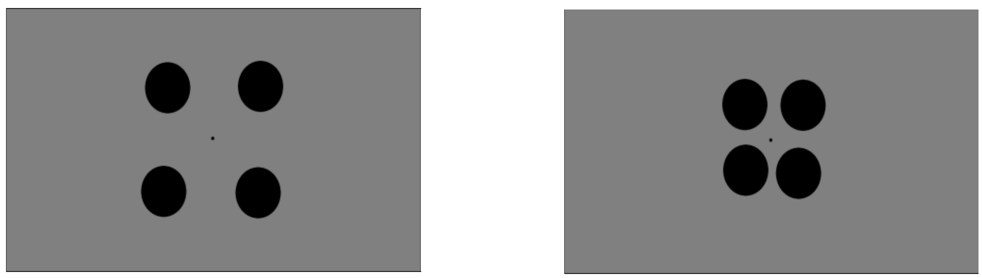

Figure 6. Comparison between Stimuli in Experiment 1 (left) and 2 (right). Note that in experiment 2 the circles are closer to the center of the screen than in experiment 1.

As in experiment 1, each of the participants' responses were recorded as either correct (if the participant correctly selected the quadrant in which the stationary circle was located) or incorrect (if the participant selected any of the other circles). If FLIIM varies across the visual field, participant accuracy will also vary across the visual field. If FLIIM is more profound in parafoveal[3] vision than in foveal[4] vision, then participant accuracy will be lower with stimuli that are presented in parafoveal vision (Figure 7). Conversely, if FLIIM is stronger in foveal vision, participant accuracy will be lower with stimuli that are presented in foveal vision (Figure 8).

[3] Parafovea: Portion of the retina that is responsible for peripheral vision.
[4] Fovea: Central portion of the retina that is responsible for the sharp reception of the center of the visual field.

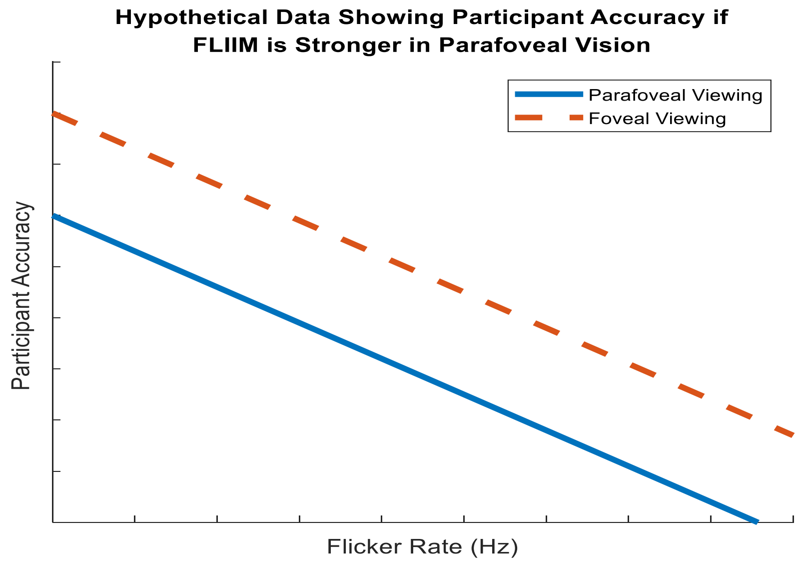

Figure 7. Hypothetical Data Showing Participant Accuracy if FLIIM is Stronger in Parafoveal Vision. If FLIIM is stronger in parafoveal vision than in foveal vision, participant accuracy will be lower with stimuli that are presented in parafoveal vision.

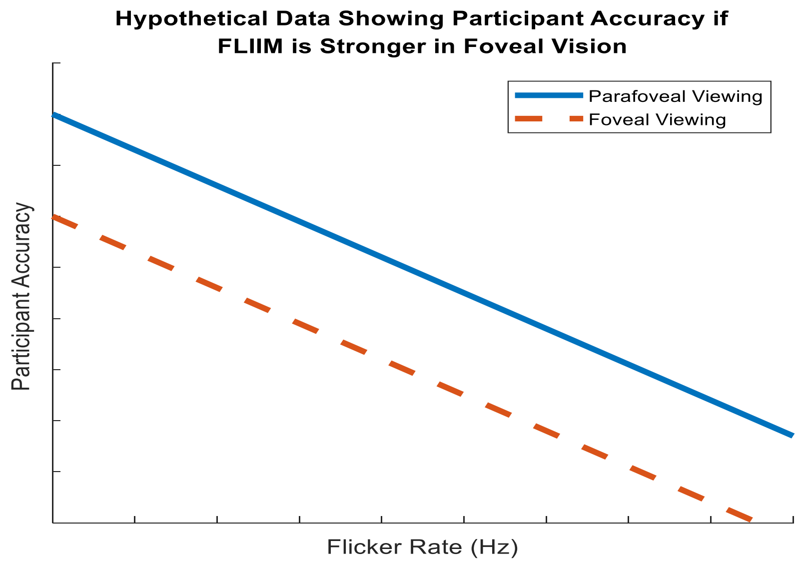

Figure 8. Hypothetical Data Showing Participant Accuracy if FLIIM is Stronger in Foveal Vision. If FLIIM is stronger in foveal vision than in parafoveal vision, participant accuracy will be lower with stimuli that are presented in foveal vision.

Experiment 3

In order to determine whether FLIIM occurs with isoluminant stimuli, each participant completed a color calibration in the setup for the experiment. This calibration was divided into two parts, one that determined the participants' isoluminant red RGB[5] values relative to the background and a second that determined the participants' isoluminant green RGB values relative to the background.

In this calibration, four circles were set to flicker at 10 Hz and were displayed on a grey background with a central fixation point. The circles' RGB color values were controlled by the up and down arrow keys, and the participant was free to utilize these keys throughout the calibration. In the red calibration, the red RGB color value could range from 0 to 255 while green and blue values remained at 0; in the green calibration, the green color value could range from 0 to 255 while red and blue values remained at 0.

The participants were asked to change the color of the circles with the arrow keys while fixating on the central fixation point. The circles were considered isoluminant to the background when their flickering was perceived to minimize or cease (Kaiser & Boynton, 1996; Kleinholdermann, Franz, Gegenfurtner, & Stockmeier, 2009). The circles also appeared to fade into the background to some participants. The participants used the arrow keys to change the color values while watching for the point at which this characteristic minimization of flicker or fading effect occurred. Once the participant found this point, a press of the spacebar saved the color values for later use. Each color

[5] RGB color space: an additive color model used in computer graphics that defines a displayed color by its levels of red, green, and blue. Each of these color levels are defined by values ranging from 0 to 255, with a higher value indicating a higher level of the corresponding color.

was calibrated three times, after which the recorded RGB color values were averaged for each color for use in the experimental stimuli.

Once the color calibration was complete, the experimental procedure was similar to experiment one (Figure 9). The four circles, each with a diameter of 140 pixels, were presented on the screen for 1000 milliseconds, over a grey background. In each trial, one circle was randomly selected to remain stationary, while the other three moved in random directions at a rate of 1 pixel per frame. In control trials the circles did not flicker, remaining a constant isoluminant red or green. In experimental trials, circles alternated between isoluminant red and green, creating a flicker effect at 2 Hz, 4 Hz, 6 Hz, 7 Hz, 8 Hz, 9 Hz, 10 Hz, 12 Hz, or 14 Hz. The participants were prompted to determine in which quadrant the stationary circle was located, and their responses were recorded as either correct (if the participant correctly selected the quadrant in which the stationary circle was located) or incorrect (if the participant selected any of the other circles) for later analysis.

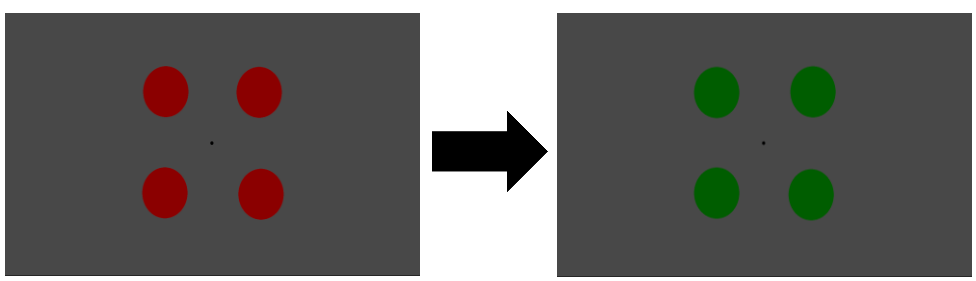

Figure 9. Example of Two Consecutive Frames of Experiment 3 after Calibration. Between frames the circles have changed from red to green, and three of the circles have moved by 1 pixel in a random direction. In the next frame, the circles change back to red , creating a flicker effect, and the three moving circles again shift 1 pixel in a random direction.

As in experiments 1 and 2, each of the participants' responses were recorded as either correct or incorrect, and reduced accuracy in the task indicates the presence of FLIIM. If FLIIM does not occur in isoluminant stimuli, and the stationary circle is easy to identify, then participant accuracy will be at or near 100%. Alternatively, if FLIIM does occur with isoluminant stimuli, participant accuracy will follow the same trend as in experiment 1.

Results

In experiment 1, participant accuracy was lowest at 2 Hz but increased gradually as the flicker rate increased. Recall that FLIIM makes the stationary circle difficult to discern, leading to a decrease in participant accuracy when FLIIM is occurring. Because, participant accuracy was lowest at 2 Hz, FLIIM was most profound at 2 Hz (Figure 10). As tested in experiment 2, participant accuracy was overall higher across all flicker rates in foveal vision (approximately 20% higher at 2Hz), but was still lowest at 2Hz. Using the same logic, lower participant accuracy in parafoveal vision indicates that FLIIM is most profound in parafoveal vision (Figure 11).

To further investigate these effects, a 2 × 10 repeated-measures ANOVA was performed, revealing a significant within-subjects main effect of frequency, $F(3.448, 58.617) = 29.467$, $p < 0.001$, and a between subject main effect of position in the visual field $F(1, 17) = 5.002$, $p < 0.04$. Also found was an interaction between frequency and position in the visual field $F(3.448, 58.517) = 2.894$, $p < 0.037$ (Figure 12). T-tests comparing foveal and parafoveal vision were significant only for 2 Hz, 4 Hz, and 7 Hz, frequencies at which FLIIM is strongest.

Participant accuracy was overall lower with isoluminant stimuli. Participant accuracy was still lowest at 2 Hz and increased as the flicker rate increased. In order to verify that participant accuracy deficits were not due to chance, a repeated-measures ANOVA was performed, revealing a significant within-subjects main effect of frequency in isoluminant stimuli, $F(3.144, 21.156) = 13.108$, $p < 0.001$. The significance of the main effect indicates that FLIIM is conserved with isoluminant stimuli (Figure 13).

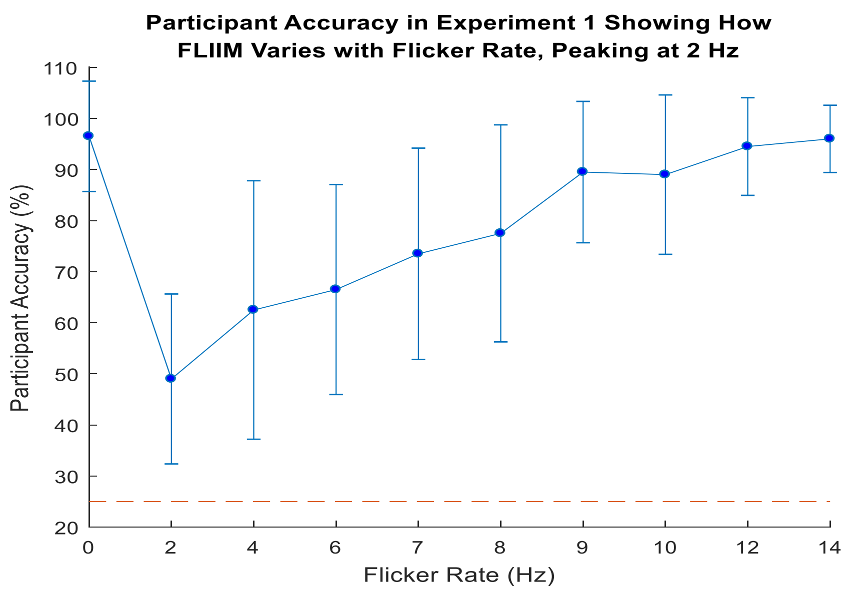

Figure 10. Participant Accuracy in Experiment 1 Showing How FLIIM Varies with Flicker Rate. In parafoveal vision, FLIIM was most prominent at 2 Hz and weakened as flicker rate increased. Note that the dotted line at 25% indicates the level of accuracy that would be achieved if participant responses were made at random.

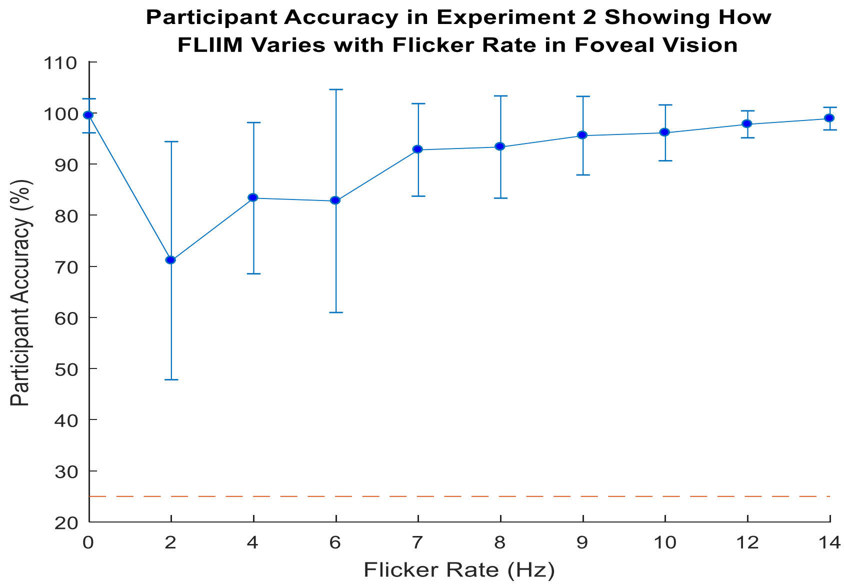

Figure 11. Participant Accuracy in Experiment 2 Showing How FLIIM Varies with Flicker Rate in Foveal Vision. While overall participant accuracy was higher than in parafoveal vision, FLIIM was still most prominent at 2 Hz.

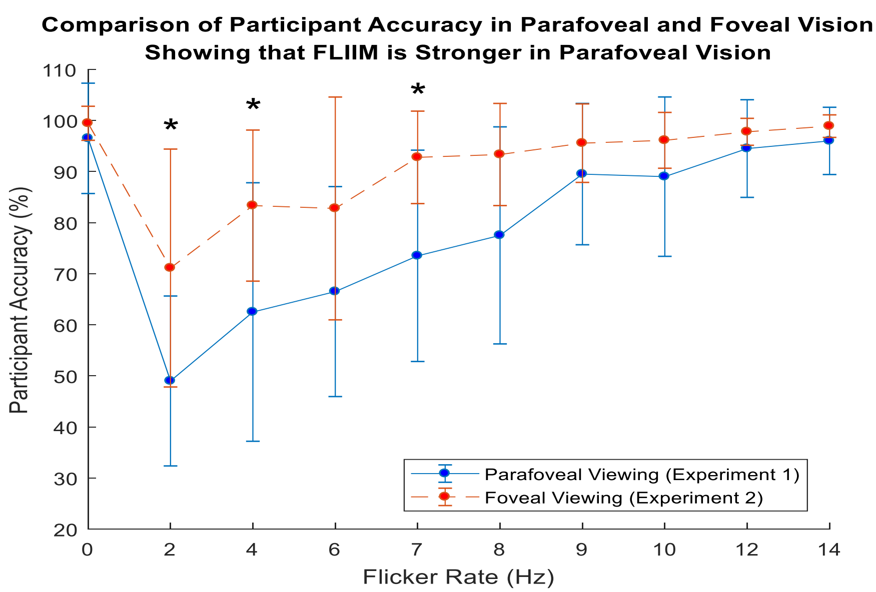

Figure 12. Comparison of Participant Accuracy in Parafoveal and Foveal Vision Showing that FLIIM is Stronger in Parafoveal Vision. Stars at 2 Hz, 4 Hz, and 7 Hz indicate significant differences between response rates in foveal and parafoveal viewing.

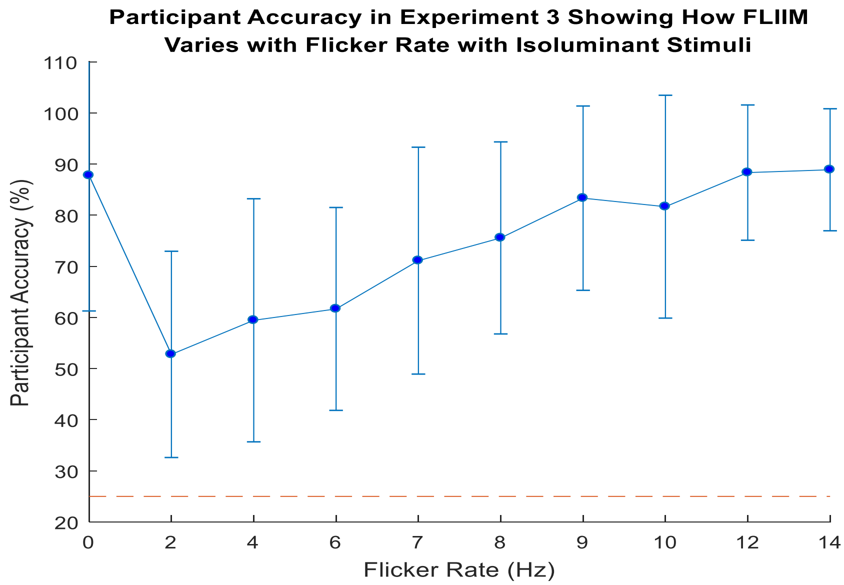

Figure 13. Participant Accuracy in Experiment 3 Showing How FLIIM Varies with Flicker Rate with Isoluminant Stimuli. Overall participant accuracy was lower than earlier experiments. Like earlier experiments, FLIIM was strongest at 2 Hz.

Discussion

As anticipated in Figure 5, FLIIM was strongest at a specific frequency (2 Hz) rather than being directly proportional to flicker rate (Figure 14). Also, as the flicker rate was increased, FLIIM effects sharply declined. This decrease in illusory motion at higher flicker rates can likely be explained by the flickering stimulus approaching the flicker-fusion threshold. Presumably, as the stimulus reached the flicker-fusion threshold, flicker would be imperceptible and FLIIM would be eliminated. This trend was conserved for both alternating luminance and isoluminant stimuli, in both foveal and parafoveal vision. While it was originally anticipated that FLIIM would be strongest between 7-10 Hz, further experiments could be performed to more precisely identify the optimal flicker rate at which FLIIM is observed, most likely somewhere between 1-3 Hz.

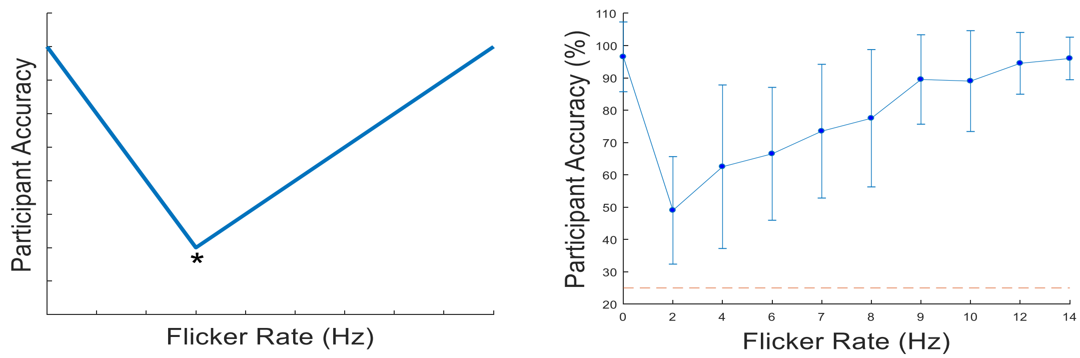

Figure 14. Comparison of Hypothetical Data Showing an Intermediate "Optimal" Flicker Rate for FLIIM and Results from Experiment 1. Note that participant accuracy decreases until the "optimal" flicker rate is reached, after which participant accuracy increases.

Understanding why flicker-induced induced motion is most profound at 2 Hz may hint at the temporal tuning characteristics of higher order motion perception. Because neuronal firing rates are dynamic and tunable (Drion, O'Leary, & Marder, 2015; Rinzel & Ermentrout, 1998), it is unlikely that flicker-induced induced motion occurs due to some isolated limitation in one or more types of neurons. Rather, it is more likely that FLIIM occurs as a perceptual resolution of ambiguity that is brought about by some nuance in how one or more populations of neurons encode and communicate a stimulus to upstream neurons. One way this ambiguity may manifest is in the spike trains[6] produced to encode a stimulus with 2 Hz of flicker. Because it is not completely understood how changing spike trains correlate to the information they encode (Rocha, Doiron, Shea-Brown, Josić, & Reyes, 2007; Svirskis, Hounsgaard, 2003), it is possible that the timing of neuronal spikes that are created in response to 2 Hz of flicker in the visual cortex send an ambiguous signal somewhere upstream. Due to this ambiguous

[6] Spike train: A series of signals that are sent by neurons to represent the information they encode. Similar to Morse code, the rates at which different parts of the signals are sent represent the information encoded.

signal, it is difficult to perceptually discern what objects in the visual field are moving and flicker-induced induced motion is experienced.

Another possible way that this ambiguity may manifest is in the combined signals of multiple types of neurons within the visual cortex. For example, direction- and motion-sensitive neurons may respond incongruously to stimuli that flicker at 2 Hz compared with other, more static stimuli. Together, the incongruous message they forward to upstream neurons may lead to the ambiguity that manifests in perceived motion.

As was anticipated in Figure 7, participant accuracy was lower with stimuli located in parafoveal vision, indicating that FLIIM is strongest in parafoveal vision (Figure 15). The interaction found between foveal and parafoveal viewing was frequency specific: at 2 Hz, 4 Hz, and 7 Hz. These were frequencies at which FLIIM was strongest, indicating that the portion of the visual field in which the flickering stimuli are presented specifically impacts the strength of FLIIM, rather than the difficulty of the task itself.

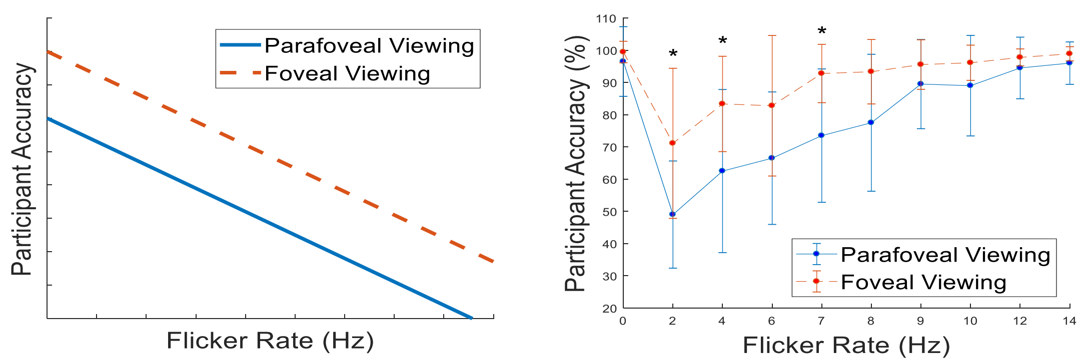

Figure 15. Comparison of Hypothetical Data Showing Participant Accuracy if FLIIM is Stronger in Parafoveal Vision and Data from Experiments 1 and 2. In both the hypothetical and actual data, participant accuracy is lower in parafoveal vision, indicating that FLIIM is strongest in parafoveal vision.

One explanation for this interaction is that FLIIM vari across different populations of visual cells due to the physiological variation within cellular populations. Alternatively, the discrepancy in FLIIM strength between foveal and parafoveal viewing may be explained by the foveal stimuli being close enough together to allow the moving objects or fixation point to act as references for the nonmoving object, thereby eliminating ambiguity, increasing participant accuracy, and decreasing measured FLIIM strength.

Participant accuracy was overall lower when utilizing isoluminant colored stimuli than when utilizing alternating luminance stimuli. However, the trend in participant accuracy was very similar to luminance experiments (Figure 16). The preservation of significant FLIIM strength at 2 Hz when utilizing isoluminant stimuli indicates that FLIIM occurs in both first- and second-order motion perception. Because FLIIM is active in both first- and second-order motion perception, and both first- and second-order motion perception converge at hMT+, FLIIM may occur in hMT+ or further downstream. This would be consistent with classical induced motion illusions such as the Duncker illusion.

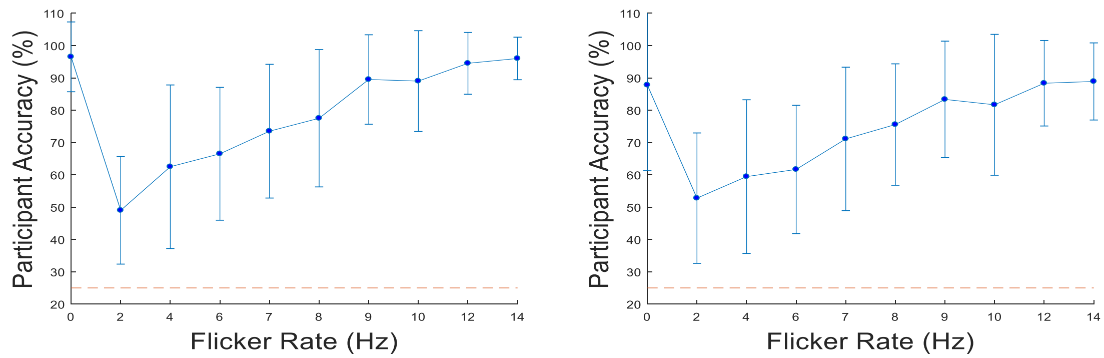

Figure 16. Comparison of Participant Accuracy Utilizing Alternating Luminance and Isoluminant Stimuli. Alternating luminance data from experiment 1 is on the left, isoluminant data from experiment 3 is on the right. Overall participant accuracy is decreased with isoluminant stimuli, but the "optimal" flicker rate at which FLIIM occurs, and the surrounding trend, is conserved between stimuli types.

Conclusion

This project has provided evidence that flicker-induced induced motion varies with flicker frequency, and that there is a peak frequency at which FLIIM occurs. FLIIM magnitude also varies across the visual field, with FLIIM effects becoming negligible as flickering stimuli are moved closer to foveal vision. These findings allow for the reproducible creation of FLIIM and further investigation of its mechanics. The parameters defined in this project also allow researchers to avoid unwanted flicker-induced induced motion in their stimuli, preventing potentially unwanted effects.

This project also found that FLIIM is present for both first- and second-order motion perception. Because the early processing of first- and second-order motion perception is located in separate pathways, FLIIM likely occurs later on in the visual system. The neural correlate of classically defined induced motion, hMT+, is a good candidate for the neural correlate of flicker-induced induced motion because it integrates both first- and second-order motion information. However, more research must be conducted to determine the precise neural properties that cause FLIIM to be most pronounced at 2 Hz.

The quantification conducted in this project adds flicker-induced induced motion to the list of defined induced motion effects. Meanwhile, understanding FLIIM broadens our understanding of how flicker can impact the visual system. Further research of FLIIM may hint at the temporal tuning characteristics of higher order motion perception. The findings outlined in this project help refine future models of motion perception and other models that utilize flickering stimuli.

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