The Flash-Lag Effect: An Eye Tracking and Pupillometry Study of Simultaneity

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The flash-lag effect (FLE) is a prime example of the perceptual problem of time representation. The effect appears to be a temporal perceptual violation of simultaneity that occurs whenever a flash (i.e., sudden and brief) stimulus happens to be physically aligned in space and time with a constantly moving object. This study aims to contribute to the FLE phenomenon by focusing on attention (i.e., as indexed by pupil dilation) and hemispheric specialization (i.e., as indexed by visual hemifields' differences). The main purposes of this thesis were: 1) To study how visual processing deals with motion interpolation. 2) To investigate whether pupillary responses and eye movements can index mental effort during the FLE task. 3) To investigate or confirm functional asymmetries (e.g., Strong et al., 2019) across left (LVF) and right visual fields (RVF) in terms of motion stimuli processing. Statistical analysis on performance and the effect of asynchrony of motion and flash replicated the classic effect. In addition, they showed interesting differences across visual fields, reaching a significant advantage in the LVF than in RVF in response time and a marginal, non-significant, effect in accuracy. Further, results showed that pupillary responses can index mental effort and hemispheric differences since participants had a tendency to larger pupils in the LVF compared to RVF.

Moreover, contrary to previous studies, which claimed that the FLE is not affected by attentional deployment, our study suggests that participants are more engaged with attention (i.e., larger pupils) in the LVF. In addition, results provide a visual field and lag interaction for response time: participants were more accurate, and faster.

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"All our sensible experiences, as we get them immediately, do thus change by discrete pulses of perception… they come to us in drops. Time itself comes in drops"

(James, 2009, p. 83)

Abbreviations

A1: Primary auditory cortex

AIC: Akaike information criterion

BF: Bayesian Factor

FLE: Flash-lag effect

LC: Locus coeruleus

LGN: Lateral geniculate nucleus

LVF: Left visual field

LH: Left hemisphere

MST: Medial superior temporal

MT: middle temporal area

NE: norepinephrine

PSE: Point of Subjective Equality

RH: right hemisphere

RTs: Response Times

RVF: Right visual field

V1: primary visual cortex

V5/MT+: middle temporal visual area

VEPs: Visual evoked potentials

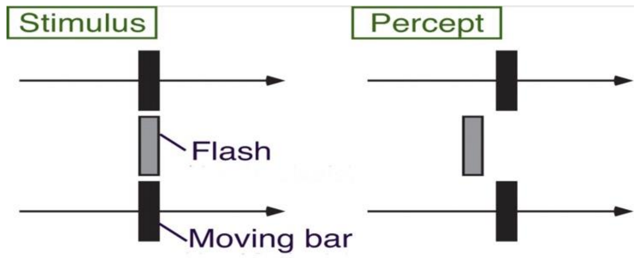
1. Introduction

For a long time, crystal balls were believed to have mystical forces to allow people to see the future. However, new research suggests that the ‘crystal balls’ that give us visions about the future may be in our eyeballs (and brain; Changizi, 2010).

At least since the studies of Helmholtz and Wundt, cognitive scientists have been investigating our brain's ability of timekeeping and how these relate to our conscious perception of time (Nijhawan, 2008). In about a tenth of a second, our visual system takes light as input and transforms it into a visual perception of the world (Changizi, 2010). Knowing where things are and at what time is extremely important for survival. For example, a person needs to localize the initial location of a hand, as his arm moves to shake another’s hand. Our other motor tasks, such as walking and driving, also rely on timed motor movements that are on the sub-second scale. Changizi (2010) points out that the purpose of our brains is not only to perceive objects that stimulate our retina but eminently to know their direction in relation to us (to our left or right, front or back). Indeed, the relative position of an object in motion constantly changes compared to the perceiver's relative position in the real world. The weak and often unreliable sense of timing that our conscious minds make explicit is even more surprising since in other ways our brains prove to be highly accurate chronometers when considering the unconscious control of bodily movements (Changizi, 2010).

However, we should consider that all neural processes have inherent time delays (Nijhawan, 2008). The most important requirement of the visual system is to provide accurate information about the position of an object in the visual field especially when the object and/or observer are moving (Nijhawan, 2001). Given the neural delay in transmission of signals within the brain, many researchers and studies have focused on the brain’s ability to ‘compensate’ for such transmission delays that allow us to perform a behaviour successfully. For example, think about catching a ball thrown at you at the speed of ten meters per second. Without the use of future-seeing to compensate for the brain delay, the ball might have moved around twenty-five degrees, which is almost one meter in space, before cortical areas receive direct input about its movement (Changizi, 2010). Specifically, in order to understand how we cope successfully with the above situation and ultimately catch the ball, we should answer the question why we perceive illusions. Although most of the psychological literature on optical illusions suggested the idea that illusions reflect the efforts of our brain to create appropriate perceptions fit for a world that is three-dimensional (Gregory, 1998), we will take a different take here. Optical illusions are typically on such flat surface (i.e., paper) but they may betray attempts to interpret these on the basis of our knowledge of a three-dimensional world. An alternative view, championed by Changizi (2010), suggests that all optical illusions may instead reflect our brain's 'future seeing' so that the brain creates perceptions that are re-calibrated with the actual moment despite they have not happened yet.

1.1 Defining Flash-Lag Effect



[1]**Figure 1.** Flash-lag effect illustration

The flash-lag effect (FLE) is a prime example of the perceptual problem presented above and it is also the focus of the empirical investigation that is reported in this thesis. The

[1] From Murakami, 2001, p.126. Stimuli consists of two vertically aligned vertical bars moving from left to right, and the flashed object consists of a vertical bar flashed between the targets.

effect appears to be a temporal perceptual violation of simultaneity that occurs whenever a flash (i.e., sudden and brief) stimulus happens to be physically aligned in space and time with a constantly moving object (Hazelhoff, 1924; MacKay, 1958; Mateeff & Hohnsbein, 1988; Nijhawan, 1994). In everyone's perception, the flash appears in a delayed position in time compared to the moving object (Nijhawan, 2002) although the experimenters set up the displays so that the two events, flash and object, are actually in the same position at the same time. The phenomenon was first described in the nineteenth century (Hazelhoff & Wiersma, 1924; MacKay, 1961; Mateef et. al., 1981) but it was recently revived by the work of Nijhawan, Eagleman, Shimojo, and others.

There are two general ways known to assess if there is a FLE. The first way is for participants to decide if the flashed object was shown before or after the moving object passed the location of the flashed object (e.g., is the flashed object located to the left or right side of a horizontally moving object?) (Whitney et al., 2000), or when the flash object is presented, is the moving target crossing or approaching the flash object (e.g., was the target behind or in front of the flash object?) (Moore & Enns, 2004).

The other way is the adjustment method (zeroing procedure) where participants adjust the flashing object presentation relative to the moving object until the two stimuli appear to be simultaneously in the same place (Lappe & Krekelberg, 1998). The first FLE type of effect was observed by Ernst Mach (1885,1897) as a spark or flash that happens during the alteration of a saccadic eye movement. In a stroboscopically-bright visual field, MacKay (1958) introduced a self-luminous and a non-luminous object and moved the eye passively, and he reported that the stroboscopically-bright object lagged the self-luminous object (similar effect recorded by; Mitrani & Dimitrov, 1982; Mateeff & Hohnsbein, 1988). Nevertheless, it is with the rediscovery of this effect by Nijhawan (1994) that an explosion of interest arose in FLE. In this experiment, stimuli consist of a bar rotating clockwise and an unpredictably flashing segment in perfect alignment with the rotating bar. Nijhawan observed that position of the flashed segment lagged behind the moving target so that the extended line looked broken, though it was always a straight line. In another experiment, Nijhawan (2008) presented, a light bulb flashed whenever a moving ball passed it. Even though this is what physically happened, observers perceived the ball as being beyond the flash at the time this occurred. Since the flash appeared to lag behind the ball, that perceptual phenomenon was named as the flash-lag effect. The main reason this simple demonstration caused an explosion of interest is that understanding the phenomenon leads us to understand in detail how the sensory-motor system adjusts for perception delays due to neural processing times (Nijhawan, 2008).

1.3 Possible Accounts of The Phenomenon

Motion Extrapolation Theory*:* Nijhawan (1994) hypothesized that FLE takes place because the visual system extrapolates a moving object's direction to compensate for perceptual delays due to the neural process time. In other words, the direction of a moving target is being extrapolated forward in time and space (Nijhawan,1994; Maiche et al., 2007; Maus & Nijhawan, 2008). In real life, the movements of objects (e.g., a thrown ball) is highly predictable, but the flash is an unpredictable, event. Hence, its perception cannot be represented in advance or extrapolated and therefore it happens in a tenth of a second after it occurs as visual information needs this time to reach high-level areas within the visual system of the human brain (Changizi, 2010).

Motion Interpolation Theory: Contrary to the extrapolation theory, when it is known the direction of the object, an interpolation mechanism would ‘fill in' the trajectory of the object in a retroactive manner, by interpolating the object's previous location with the knowledge of its present position (Wertheimer, 1912; see also Shioiri et al., 2000; Hogendoorn et al., 2007).

Representational Momentum: In the 1980s, psychologist Jennifer Freyd found a related phenomenon that she labelled "representational momentum". She showed participants basic movies of a moving rectangle that suddenly stopped and asked them, alter, what they recalled about the final frame or the final position of the rectangle. As a result, the final frame was incorrectly remembered by participants as further along from its translation than it really was, as if its interruption provided a signal to terminate the extrapolation of motion, which however remembered as in a position yet to be reached.

Attention Shift Theory: This account suggests that the flash-lag effect happens because attention is primarily focused on moving target and once the flashed object is displayed, attention is switched subsequently towards the flashed object. This transition of the attentional 'spotlight' requires time, but the target proceeds to move through this time. At the moment the flashed object is seen, attention has already tracked the target some considerable distance and therefore the flashed object is registered as lagging behind the moving target. Attention shift theory is consistent with target velocity (Nijhawan, 1994) and flashed object predictability (Baldo & Namba, 2002).

Differential Latency Theory: According to differential latency theory, a moving target is processed more rapidly than a static flashed object, and hence the moving target reaches more rapidly perceptual awareness. Thereby, if a flashed object and a moving target are synchronized, the processing time for the flashed object will be in excess to the moving target (Ögmen et al., 2004; Whitney et al., 2000; Mateeff & Hohnsbein, 1988; Baldo & Klein, 1995; Purushothaman et al., 1998; Whitney & Murakami, 1998; Whitney et al., 2000).

Fröhlich effect: When a moving object suddenly appears through a static aperture, the object's initial position appears to be shifted in the motion direction (Fröhlich, 1923), as in FLE (MacKay, 1958; Nijhawan, 1994). Some of the mechanisms suggested for FLE are similar to those proposed for the Fröhlich effect, for example, the required time for attention shift for the flashed object (Baldo & Klein, 1995) or moving target (Müsseler & Aschersleben, 1998). Therefore, FLE and the Fröhlich effect are thought to be caused by the same mechanisms (Kirschfeld & Kammer, 1999; Eagleman & Sejnowski, 2007).

However, what seems unclear from the above accounts is whether FLE is a temporal or a spatial effect. Theories based on motion extrapolation theories (Nijhawan, 1994, 2008) or ‘postdiction’ (e.g., Eagleman & Sejnowski, 2002), propose that FLE is a spatial phenomenon. Furthermore, theories based on latency differences (e.g., Whitney & Murakami, 1998; Whitney & Cavanagh, 2000), as well as some types of postdiction (Whitney, 2002; Ichikawa & Masakura, 2006) interpret it as a temporal phenomenon. Indeed, FLE was described by Murakami (2001) as a spatiotemporal correlation structure, where a flashed object's previous spatial location is compared to a current spatial position of moving object. FLE is generally evaluated in terms of the spatial offset, which happens between the flashed object and moving target (Kreegipuu & Allik, 2004). In sum, both temporal and spatial information are involved in FLE, but the relationship is not univocal.

Another question is whether FLE occurs because of a mislocalization of the absolute location of the flashed object or of the moving target. According to some scholars, the lag of the flashed object happens because of a mislocalization of the moving object (Hubbard, 2008; Becker et al., 2009; Changizi, 2010). According to this, FLE could be a second-order or derived perception that arises from more simple illusions involving the flashed object and moving target's presumed absolute locations (Shi & de’Sperati, 2008; Maus & Nijhawan, 2006, 2008, 2009; Rotman et al., 2004, 2005).

1.4. Characteristics Affecting Flash-Lag Effect

Based on the theoretical proposals mentioned above, some factors considered to influence FLE (Hubbard, 2014) are categorized as observer's characteristics such as eye movements, gaze fixation, perceptual set, attention distribution, and conceptual knowledge. In addition, stimuli's characteristics such as eccentricity, duration of a flashed object, distance between the flashed object and moving target, and target direction.

1.4.1 Characteristics of the Observer

***Eye movements and gaze fixation*.** Nijhawan (2001) used a flashed disk inside an annulus rotating through a circular motion. A FLE occurred when participants fixated the centre point of the circular motion or fixated the place where the flashed object would be displayed. Consequently, if participants followed the movement within the annulus, FLE was reduced. If participants can track a moving target with smooth pursuit, then FLE is eliminated (Nijhawan, 2001). When flashed objects are displayed during an eye movement, a FLE still occurs (Blohm et al., 2003; Nijhawan, 2001). A *cross-modal FLE* was recorded in visual-auditory displays by Alais and Burr (2003), however, the different neural latencies might not completely explain the auditory and audio-visual FLE (Arrighi et al., 2005). Another cross-modal FLE is reported by Nijhawan and Kirschfeld (2003): if participants shifted their (non-visible) hand in a darkened setting and a visual flash was presented, a FLE may result and from either passive or active body movement.

***Perceptual set*.** An effort to interpret the present by the visual system is characterized by making a perceptual forecast (Ramachandran & Anstis, 1990; De Valois & De Valois, 1990). If participants have a perceptual set (e.g., when they are certain a flashed object will be presented rather than being uncertain) to attend the flashed object, FLE decreases (Gauch & Kerzel, 2009). In sum, the perceptual set helps to distinguish FLE from illusions that are not affected by expectation and knowledge (e.g., illusory contours), but not from mislocalizations, which can be affected by expectation and knowledge, (e.g., representational momentum) (Hubbard, 2014).

In addition to the perceptual set, the perceptual organization also can have an effect on FLE. In Watanabe et al.'s (2001) study, a moving target was presented in different organizations (i.e., one and two square, and two and four parallel vertical bars; first two and last two in different colours) in order to influence perception. FLE increased at the front edge (i.e., first of four-bar) and reduced at the back edge (i.e., fourth bar) of the moving target (Watanabe, 2004; Watanabe et al., 2001). Thus, the brain seems capable of complex mental calculations, resulting in efficient visual perception.

Attention Distribution. Tracking a moving object requires a great amount of attention, leaving very little attention to detect the flashed object. This makes it even longer for the flashed object to reach perception, leading to a higher FLE (Nieman et al., 2006). However, Chappell, Hine, Acworth, and Hardwick (2006) proposed that the flashed object automatically captures attention. FLE increases with changes in attention over a broader distance and it increases when participants attend to several targets or tasks (Sarich et al., 2007; Shioiri et al., 2010).

Conceptual knowledge. Noguchi and Kakigi (2008) introduced moving targets and objects that are parts of Kanji letters (compared to pseudo-kanji shapes) to native Japanese speakers and non-Japanese English speakers, and their neural activities measured by magnetoencephalography. With Kanji segments, FLE for Japanese speakers decreased. FLE decreased if the stimulus was semantically relevant (Noguchi & Kakigi, 2008). Furthermore, for Kanji-knowledgeable participants' initial brain response occurred as early as 160 msec after the flashed object was introduced.

1.4.2 Characteristics of the Stimuli

Presentation timing of the flashed object. FLE occurs with *flash-initiated* (when the flashed object is displayed at the target motion onset) and *flash-midpoint* (more consistent with flash-initiated and flash-terminated) displays, but not with flash-terminated displays (i.e., when the flashed object is displayed at the target motion offset; Eagleman & Sejnowski, 2000; Khurana & Nijhawan, 1995; Nijhawan et al., 2004; Watanabe, 2004).

Eccentricity. The eccentricity of the moving and flashed bar appears to contribute to FLE (Kanai et al., 2004). If the retinal eccentricity of the flash increases, the flash-lag increases as well (Baldo & Klein, 1995). Although, it decreases if the moving target is more eccentric (Linares et al., 2007).

Duration of the flashed object. FLE happens with constant flashed object with a duration under 80 ms (Brenner & Smeets, 2000; Eagleman & Sejnowski, 2000) and up to 500 ms (Lappe & Krekelberg, 1998; Krekelberg & Lappe, 1999).

Distance between flashed object and moving target. FLE increases if distance increase between flashed object and moving target (Baldo & Klein, 1995; Baldo, Kihara, et al., 2002; Kanai et al., 2004)

Target direction. FLE increases if the target moves toward fixation (Mateeff et al., 1991; Kanai et al., 2004; Brenner et al., 2006; Shi & Nijhawan, 2008).

2. The Present Flash-Lag Study

In order to understand, on one hand, the limits and restrictions of human perception and on the other hand, the assumptions or ‘priors’ used by the brain in making sense of the world, visual illusions (e.g., FLE), are very powerful tools. In the FLE, as explained in detail in the previous section, visual moving stimuli seem ahead of their actual position in relation to an unpredictable flashed object. This illusion highlights a significant aspect of the visual system: unlike computers, neuronal signals move at a comparatively slow speed (Khoei et al., 2017). The resulting delays are generally considered as the source of the flash's perceived spatial delay. However, after years of discussion, there is no consensus yet to explain the underlying mechanisms. Thus, this study aims to contribute to the FLE phenomenon by focusing on the attention (i.e., as indexed by pupil dilation) and hemispheric specializations (i.e., as indexed by visual hemifields' differences).

2.1 Visual hemifields

Because of neuronal activity that occurs through a distributed network of cortical regions, visual motion processing is accomplished in a specific region responsible for processing subtly distinctive features of moving visual scene (Braddick et al., 2000; Beauchamp et al., 2002). In the human brain, this region is called (h)V5/MT+ and is located in the lateral occipitotemporal cortex (Vaina, 1989). Area MT (in short) appears to be a key region (McKeefry et al., 1997; Culham et al., 2001) for the conscious perception of motion as witnessed by the neurological impairment of Akinetopsia (Zihl et al., 1983). The possible role of MT in the interhemispheric incorporation of motion processing through the contralateral and ipsilateral visual hemifields has been illustrated in a number of studies (Vanni et al., 2004; Akin et al., 2014). This neuroimaging work also suggests a type of right hemisphere (RH) dominance for motion processing. Intriguingly this may add to or interact with the well-known RH dominance for spatial attention.

Clinical literature showed that visual hemifield neglect and inattention are more frequently linked for right hemisphere parietal lobe lesions and are more serious or permanent compared to the left hemisphere (LH; Schenkenberg et al., 1980; Heilman et al., 1985; Bowen et al., 1999; Ringman et al., 2004; Becker & Karnath, 2007). Likewise, brain imaging studies (e.g., PET, fMRI, and ERPs) in healthy humans have also examined hemispheric asymmetries in spatial attention. Studies in brain imaging seem to support the RH superiority for spatial attention. Full-field stimuli studies (fMRI: Gitelman et al., 1999; Arrington et al., 2000; Corbetta et al., 2000; Husain & Rorden, 2003; PET: Corbetta et al., 1993; Nobre et al., 1997) reported manipulating effect for spatial attention is larger in the RH than the LH (Bosworth, 2011). Besides that, several studies have suggested relatively equal hemispheric effects of the spatial attention (fMRI: Kastner et al., 1999; Hopfinger et al., 2000; Shulman et al., 2010).

In addition to studies on brain-damaged patients, many scientific studies have compared the visual hemifields (RVF vs LVF), and bulk of the studies support the asymmetry between hemifields in terms of spatial attention. Asymmetries found in visual fields might be because of the anisotropies in the neural density of the lateral geniculate nucleus (Connolly & Van Essen, 1984), striate cortex (Van Essen et al., 1984; Tootel et al., 1988), and ganglion cell layers (Perry & Cowey, 1985).

In accordance with the idea of a RH benefit in spatial attention, several studies (Dimond & Beaumont, 1973; Whitehead, 1991) observed that it is easier to sustain attentional control for stimuli in the LVF than in the RVF (Bosworth et al., 2011). Kanai et al., (2014) used this known asymmetry to account for visual field difference, and they claimed that the right hemifield is dominant for visual attention. Their data showed that the FLE was greater in the LVF than in the RVF, yet they did not propose any specific account for the RH advantage. Bosworth et al., (2011)'s study also investigated asymmetries between visual hemifields, in terms of spatial attention effect. Their results provided another psychophysical evidence for stronger effect of spatial attention in the LVF/ RH, especially in the dorsal stream for motion processing. Consistently, Strong et al., (2019) report that the motion area in the right hemifield shows an enhanced role for the analysis of motion. On the other hand, other psychophysical experiments using spatial cueing (Carrasco et al., 2001; Cameron et al., 2002), measured motion coherence thresholds (Bosworth & Dobkins, 2002), and measured motion and orientation thresholds (Bosworth & Dobkins, 2002; Rezec & Dobkins, 2004) do not suggest any asymmetry in spatial attention between the right and the left hemispheres.

2.2 Mental Effort, Flash-lag Effect and Pupillometry

Even a simple act of attention or perception exerts a load on mental capacity and requires some mental effort. Hence, the present study hypothesized that such processes could affect the pupil response since this is a reliable measure of mental effort (Laeng et al., 2012). Although, several mental effort measures are available, e.g., cardiovascular activity, EEG, and galvanic response (Tao et al., 2019), pupillometry is a robust and easily obtainable index by use of eye-tracking.

Mental effort is the use of cognitive capacity to process knowledge (Kahneman 1973; Gopher & Donchin 1986; Yeo & Neal 2008; Kool, 2018). In order to modulate the performance in demanding tasks that individual uses cognitive resources, an accurate and non-invasive way of measuring mental effort is pupillometry (Beatty, 1977; Laeng et al., 2012).

Hess and Polt (1964) were among the first to introduce pupillometry as a test of mental activity. Furthermore, their study revealed that pupil size changes can be utilized as a direct measure of mental activity whilst solving a multiplication problem. Further research consistently found that differences in pupil size are correlated with stimuli intensity (Stelmack & Siddle, 1982) or the task complexity (Kahneman & Beatty, 1966). In a typical short-term memory test, Kahneman and Beatty (1966) observed that pupillary dilation increased as more objects were required for a recall. Recent psychophysiological studies have also shown adequate evidence demonstrating that pupil size changes offer the best possible and accurate cognitive workload index whilst performing a task (Wardhani et al., 2020; Bochynska et al., 2020). Consequently, pupil diameter has been suggested to be used either as an assessment of brain activity index (Siegle et al., 2003) or capacity usage of the cognitive system (Just et al., 2003). These results indicate task-evoked pupillary responses, reflect moment-to-moment changes in cognitive processing load and as pupil dilations relative to baseline levels (Unsworth & Robison, 2015). Thus, pupillary changes are accurate and reliable psychophysiological indicators of mental effort or attentional allocation (Alnæs et al., 2014;

Daniels et al., 2012). In other words, phasic pupillary responses reflect the intensive aspect of attention (Kahneman, 1973).

The pupil changes are believed to arise through an inhibitory effect on the parasympathetic oculomotor system by releasing norepinephrine (NE) from the locus coeruleus (LC; Wilhelm et al., 1999). Recent neuroscience studies have also confirmed that the pupil represents the activity of LC, which is the nucleus of the norepinephrine system in the brain and whose activity at a given point in time has the effect of 'energizing' the entire brain. Importantly, previous studies in humans (Pharmacological; Phillips et al., 2000) and in apes (single-cell recordings; Joshi et al., 2013) indicate a correlation between the activity of the LC-NE system and pupil diameter changes, enabling the use of pupillometry to explore task-related changes throughout the attentional states induced by LC-NE activity (Laeng et al., 2012).

As mentioned above several previous studies showed that attention to LVF requires different neural resources than RVF (Alvarez & Cavanagh, 2005; Chakravarthi & Cavanagh, 2009; Shipp, 2011). Furthermore, this difference becomes more prominent on time-sensitive attentional tasks (Mathews & Welch, 2015). Since this project is also a time-sensitive attentional study, thus the Point of Subjective Equality (PSE) was used as a dependent variable to get the best results for the lag effect on different visual fields. In psychophysics, PSE is the point within a stimulus dimension where an observer assesses a variable stimulus (auditory, visual, tactile, etc.) to be equivalent to a standard stimulus (Vidotto et al., 2019). Additionally, the PSE is a sequence of two stimuli that the observer perceives as subjectively the same. (Schwartz & Krantz, 2018). For example, the experimenter can introduce a stimulus with a unique brightness, and then the participant will have to adapt another stimulus that is equally bright to the first one. PSE is also a measure that is independent of whether one adjusts the time variable or when time is manipulated systematically. Since time is adjusted in this experiment, PSE is a strong measurement for this study also. In sum, PSE is a strong tool for measuring the strength of an illusion (Schwartz & Krantz, 2018).

Stimulus	Flash-lag effect	Sources
Moving and flashed object	Around 30ms	(Kanai et al., 2004)
Rotation line	100ms	(Nijhawan, 2008)
Moving and flashed object	45ms	(Whitney and Murakami, 1998)
Moving and flashed object	80ms or less	(Nijhawan, 1994; Baldo & Klein, 1995; Prushothaman et al., 1998; Whitney et al., 2000; Krekelberg and Lappe, 2000, 2001)
Moving and flashed object	Around 67ms	(Watanabe et al., 2010)
Moving limb and flashed dot	94ms (foot joint) 82ms (hand joint)	(Su & Lu, 2017)
Moving ring and flashed disk	80ms	(Eagleman & Sejnowski, 2000)
Rotating disk and flashed object	60ms	(Brener and Smeets, 2000)

Table 1. Some selected previous FLE studies

2.3 Current Study

There are important empirical and theoretical implications to answer the question that how our brain compensates for differing neural processing times so that we can interact successfully with dynamic objects in real-time. A novel question is whether monitoring the eye pupils during the FLE can have something to say about the working way of our brain during such processing. To the best of our knowledge, there are no studies that have applied pupillometry to the flash-lag effect studies, although there are a few previous applications in the study of optical illusions (e.g., Laeng & Endestad, 2013) and bistable perception (e.g., with the Necker cube or binocular rivalry; Sato et al., 2020; Hovey et al., 2020) Thus, in this study, we used an infrared eye tracker to apply the pupillometry method to the flash-lag paradigm (cf., Nowak et al., 2014).

Since a flash-lag effect task can present cognitive challenges that rapidly differ during neural processing, one expectation is that changes in pupillary diameter occur in the eyes of participants if the FLE required effort more so in certain conditions than others. Indeed, several previously mentioned theories such as motion extrapolation, motion interpolation and differential latency theory assume considerable visual processing behind the FLE. Furthermore, previously mentioned studies showed the effect of attention on FLE, moreover how this effect differs across visual fields.

Specifically, the present study had the following main goals.

1) To study how visual processing deals with motion interpolation.
2) To investigate whether pupillary responses can index mental effort during FLE task.
3) To investigate or confirm functional asymmetries (e.g., Strong et al., 2019) across left and right visual fields in terms of motion stimuli processing.

In order to investigate the above purposes in the experiment an animation presented, which consist of a fixation point and, moving and flashed object (see ***Figure 2***), while an eye-tracker apparatus recorded participants' pupil size and eye movements. In the first block, the stimuli were presented on the left side of the screen for half of the participants and the opposite for the other half of participants, thus allowing the use of the divided-visual-fields paradigm (Banich, 2003; Bourne,2006) and in a counterbalanced manner. Furthermore, the time lag was manipulated in this experiment as in previous ones across several positive or negative lags besides actual simultaneity (i.e., 0 lag). Hence, time lag, visual fields, and moving and flashed object were independent variable and accordingly pupil responses, duration of eye-fixations, PSE, accuracy and RTs were considered as the neurophysiological and behavioural dependent variables.

Hypotheses

1) If the right hemisphere/ LVF is superior to the left hemisphere in spatial attention and motion perception - based on the studies (e.g., Bosworth et al.,2011; Strong et al., 2019) showing an enhanced role for the analysis of motion in the LVF/right hemisphere - then there should be pupil response asymmetries across visual fields (e.g., Kanai et al., 2014), possibly reflecting the ease in motion interpolation (a mechanism that interpolating the object's previous location with knowledge of its present position).
2) If FLE task requires mental effort and if pupillary response can index the level of attention, then pupillary dilations should increase parametrically as a function of mental effort (i.e., attention) when moving and flashed object are seen on different visual fields.
3) If attention to LVF requires different neural resources than RVF (Alvarez & Cavanagh, 2005; Chakravarthi & Cavanagh, 2009; Shipp, 2011) and if this difference becomes more prominent on time-sensitive attentional tasks (Mathews & Welch, 2015), then perceptual judgement should be less affected by visual illusion on the LVF (i.e.,

accuracy/performance will be better, or the PSE should be closer to zero lag) compared to the RVF.

3. Methodology

3.1. Participants

Twenty-seven volunteers from the University of Oslo, 6 men; 21 women; age range between 20 and 38 years (M=24.29, SD=3.73), participated in the experiment, one of the participants was author. Two participants took part only in the first block of the experiment (left visual field condition). Two participants in left visual field condition and four participants in right visual field condition were excluded from pupil analyses because the rejected trials were more than 50% of whole trials (the detail is written in the below section). In the beginning 30 participants were planned to recruit because of the COVID-19 pandemic, data collection had to stopped at number 27. Participants were found through social media ads and posters. All participants were undergraduate and graduate students who had a normal or corrected-to-normal vision. All experimental procedures were in accordance with the ethical principles outlined in the Declaration of Helsinki and approved by the Committee at the University of Oslo Psychology Department. The experiment was performed in accordance with the approved guidelines of the committee and all participants provided written informed consent.

3.2 Apparatus

In this study, pupil size and gaze position were measured by a SensoMotoric Instruments RED500 (SMI, Berlin, Germany) eye-tracking system at a sampling rate of 60 Hz. This equipment can measure an eye movement at a resolution of about 0.01°. All stimuli were presented on a 22 inches LCD monitor (P2210, Dell., Round Rock, US) with a resolution of 1680 x 1050 and a refresh rate of 60 Hz. The pupil data during eye blinks detected by using peak changes on the velocity of the pupil response were interpolated using pchip interpolation. The trial including the pupil changes in more than 6 mm/s were excluded from the analysis (the average rejected trials were 2.63 ± 1.6 trials out of 10 trials). Baseline pupil size was computed as an average of data collected during the fixation period prior to stimulus onset from -500 ms to 0 ms (i.e., presentation onset). In the time course analysis, the pupil data in each trial were normalized by subtracting the pupil size at baseline pupil size from the stimulus onset, following which smoothing of each data point with ± 80 ms. Across conditions, the pupillary response was averaged from the presentation period of stulus onset until 1,000 ms.

3.3 Stimulus Presentation

The experimental stimuli consisted of one moving and two flashed horizontally vertical short lines sliding towards the fixation point, once the moving line reached to final position, all flashed and moving line disappeared. (see ***Figure 2***). The *x* and *y* coordinates of the background and objects were 0.350 and 0.365, respectively, in CIE1931 color space. The brightness of the stimuli was calibrated using a Spyder 4 Elite photometer (Datacolor Imaging Solutions, Lawrenceville, NJ), which indicated the background was 28.41 cd/m^2. The brightness of the flashed and moving bars was 71.66 cd/m^2. The visual angle of the flashed and moving bars were 1.5° x 0.1° and 1.0° x 0.1° respectively. The trajectory of the moving vertical bar was from 4.5° to 2.5° away from the center of the monitor. The bar moved horizontally toward the center of the screen and within a time of window of 500 ms, so that the moving speed was 4°/s and the flashed object was located at 2.5° x 2.75° from the center. The fixation point of 0.2° was located at the center. Each participant's chin was fixed at a viewing distance of 70 cm. The experiment was conducted in a darkroom and controlled by Experiment Center (SMI, Berlin, Germany).

3.4 Procedure

All participants were comfortably seated in front of the computer screen with a chinrest, to prevent head movements, and a standard PC keyboard positioned on the table. Before the experiment began, an eye calibration procedure was performed with a five-point display. Calibration was accepted when error values were below 0.5 mm, or in the worst case below 0.9. Before the actual task, participants were asked to complete a short practice task to make sure they understood the task correctly (e.g., keys corresponding to ‘left of’, etc.). To avoid confusion, additional verbal instructions on the task were given only when participants had difficulty understanding the comprehension task. Experiment started with practice test, which included five trials. The total number of the experimental trials was 160 (2 visual fields × 8 delays ×10 repetition). ***Figure 2*** illustrates the experimental procedure. In each trial, a central fixation point presented for 2 ms prior to the presentation of the stimulus. This central fixation point remained visible during the whole experiment. The moving bar appeared at either left/right for 50 ms and then started moving toward the center of the screen. During the animation, the flashing bar appeared for 16 ms between the two moving bar and at 8 delay conditions: -83.3, -66.7, -50.0, -33.3, -16.7, 0.0, 16.7 and 33.3 ms relative to the middle of presentation (i.e., 250ms). A zero delay indicates that in the animation the moving and flashing lines were precisely aligned. Then, participants answered with a key press whether they saw the moving bar being located either at the left or right of the flashed bars. Each trial was self-paced, and participants initiated the next trial by pressing the spacebar. This would bring on screen the fixation point for 1000 ms followed by a gaze-controlled trigger based on an AOI centered on the fixation point.

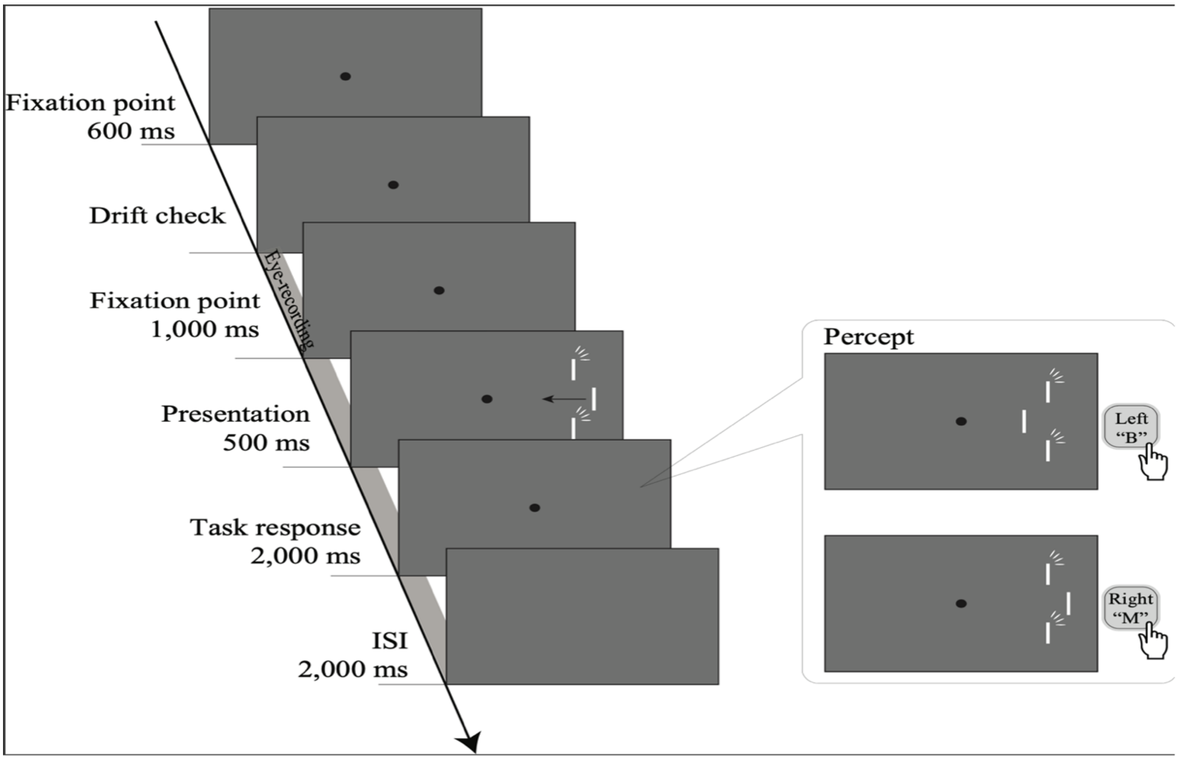


Figure 2. Experimental procedure

Each trial was separated by an inter-stimulus interval (ISI) of 2,000 ms. In the first block, the stimulus presented on the left side of the screen for half of the participants and on the right side for another half. The second block was tested by the opposite visual field from the first block, for counterbalancing condition order and allowing the use of the divided-visual-fields paradigm (Banich, 2003). Thus, total number of trials were 160 (2 visual fields × 8 delays × 10 repetition).

4. Results

4.1 Statistical Analysis

The averaged probability of participants answering whether the moving bar was perceived ahead of flashed bars was fit with a psychometric curve using a maximum-likelihood logistic function. We estimated the point of subjective equality (PSE) in the flash-lag effect at the probability of 0.5. After collecting the PSE data at left and right for all observers, we performed pairwise t-test on the PSE between the visual field. The level of statistical significance was set to $p < 0.05$ for all analyses. Effect sizes were given as partial

η^2; η_p^2 for ANOVA and as Cohen's d for t-tests. To quantify the evidence in the data, we performed Bayesian one-sample t-tests using the BayesFactor package (v0.9.12-4.2) (Morey & Rouder, 2018) for the R software (Version 3.6.3) (R Core Team, 2020). We reported Bayesian Factor (BF) estimating the relative weight of the evidence in favor of H_1 over H_0 as BF_{10}. Greenhouse–Geisser corrections were performed when the results of Mauchly's sphericity test were significant.

In the analysis of pupil response, we fitted the following two models to assess whether the pupil change variability (Y) can be explained by the lag (X) using a second-order polynomials or monotonic fitting, where β as regression coefficients.

Model 1: $Y = \beta_0 + \beta_1 X$

Model 2: $Y = \beta_0 + \beta_1 X + \beta_2 X^2$

The models were quantified using the Akaike information criterion (AIC), which specifies the evidence of goodness of fit for a model (McElreath, 2020).

Also, different standard statistical softwares (IBM SPSS, Statview) were used to obtain the mean pupillary changes related to our experimental factors (i.e., accuracy, response times and visual fields). Repeated-measures Analysis of Variance was chosen to estimate the flash-lag effect on accuracy, visual-fields, pupil change and response time. We used a repeated-measures (within-subject) design, which means that each participant performed all conditions in the experiment. However, for some conditions, we had one participant's data for one visual field but not the other, due to technical issues or poor tracking. Hence, to avoid removing a proportion of participants from the analysis, we run an ANOVA with imputation, by filling in the missing cell with the mean of the group for the same condition. Imputation constitutes an estimate of what the results would have been if there were no data loss (Allison, 2010).

4.2 Behavioral Results

4.2.1 Psychometric curve measuring the flash lag effect. The probability with which the participants chose ‘ahead’ (i.e., answering ‘Left’ for left visual field condition and ‘Right’ for right visual field condition) was calculated as shown in ***Figure 3(a)***. The average probability in each delay condition and participant was fit with a psychometric function which implements the maximum-likelihood method. ***Figure 3(b)*** shows point of subjective equality (PSE) in each visual field. The PSE was estimated by the value at the probability of 0.5. We observed the flash lag effect in both left and right visual field ($t(1, 25)$ = -4.728, p = 0, BF_{10} = 344.073, $t(1, 25)$ = -3.458, p = 0.001, BF_{10} = 19.075). The lag effect was significantly larger in left visual field than the right ($t(1, 25)$ = -2.311, p = 0.029, Cohen’s d = 0.507, BF_{10} = 1.933)

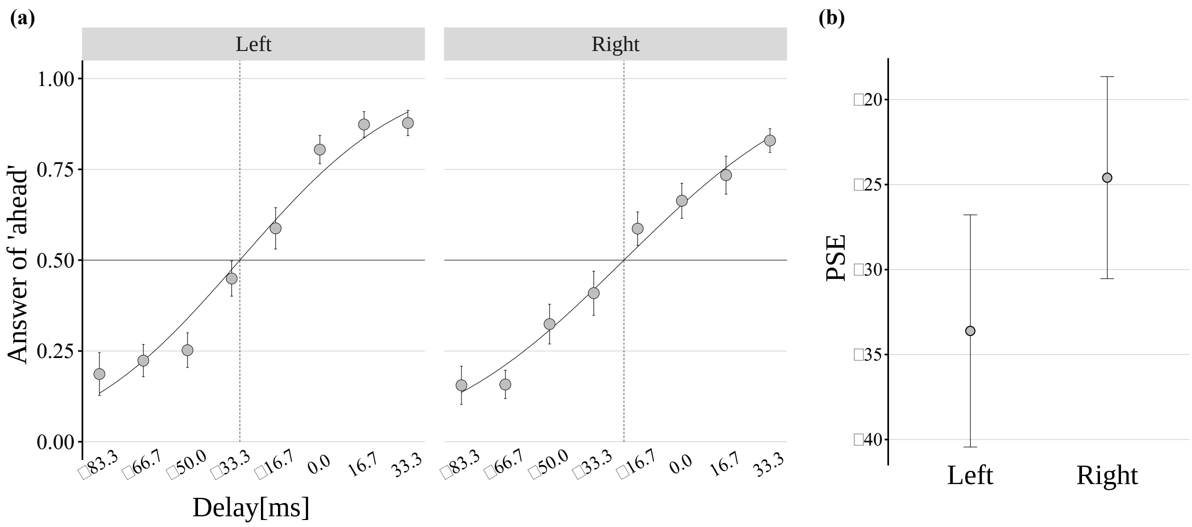


Figure 3. ***Psychometric curves for the flash lag effect.*** (a) Averaged psychometric curve for all participants. (b) Estimated point of subjective equality (PSE). Error bars indicate the standard errors of the means.

A repeated-measures ANOVA (***Table 2***) with two factors (Visual Field, Lag) was performed to investigate the effect of flash lag on Accuracy. The outcome with visual field as the between-subject factor and accuracy as the within subject factor, revealed a nearly significant result towards higher accuracy [F (1, 23) = 3.833, p =.06]. Furthermore, a second repeated-measure ANOVA with lag as the between-subject factor and accuracy as the within subject factor showed a significant effect of Delay [F (7, 161) = 3.31, $p < .001$], but no significant differences found between visual fields [F (7,161) = 1.219, p = .29], see ***Figure 4***.

ANOVA Table for Accuracy

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Subject	23	4,912	,214				
Visual Field	1	,361	,361	3,833	,0625	3,833	,454
Visual Field * Subject	23	2,163	,094				
Lag	7	23,206	3,315	82,073	<,0001	574,511	1,000
Lag * Subject	161	6,503	,040				
Visual Field * Lag	7	,255	,036	1,219	,2950	8,536	,506
Visual Field * Lag * Subject	161	4,805	,030				

Means Table for Accuracy
Effect: Visual Field * Lag

	Count	Mean	Std. Dev.	Std. Err.
LVF, -83	24	,209	,279	,057
LVF, -66	24	,220	,203	,041
LVF, -50	24	,278	,247	,051
LVF, -33	24	,439	,217	,044
LVF, -16	24	,578	,259	,053
LVF, 00	24	,778	,209	,043
LVF, +16	24	,836	,238	,049
LVF, +33	24	,868	,162	,033
RVF, -83	24	,153	,215	,044
RVF, -66	24	,150	,162	,033
RVF, -50	24	,309	,232	,047
RVF, -33	24	,399	,250	,051
RVF, -16	24	,559	,222	,045
RVF, 00	24	,637	,226	,046
RVF, +16	24	,711	,234	,048
RVF, +33	24	,799	,185	,038

Table 2. ANOVAs of the accuracy with imputation

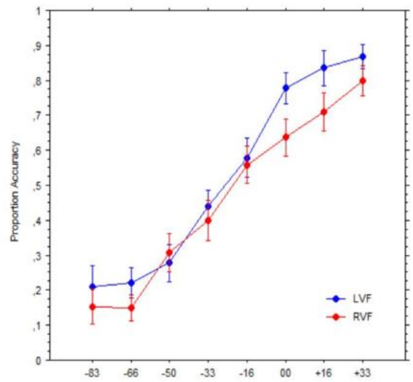


Figure 4. Accuracy means plot

4.2.2 Response times (RTs)

These were calculated from the time of stimulus offset to the participants' key presses. A two factor (Visual Field and Lag) repeated-measures ANOVA run for RTs. First repeated-measures ANOVA with Lag as the between-subjects factor and Response Time as the within subject factor (Table 3) on the average RTs revealed a significant main effect of Delay [F (7, 168) = 6,528, $p < .001$, $\eta^2_p = 0.157$] (see ***Figure 5***).

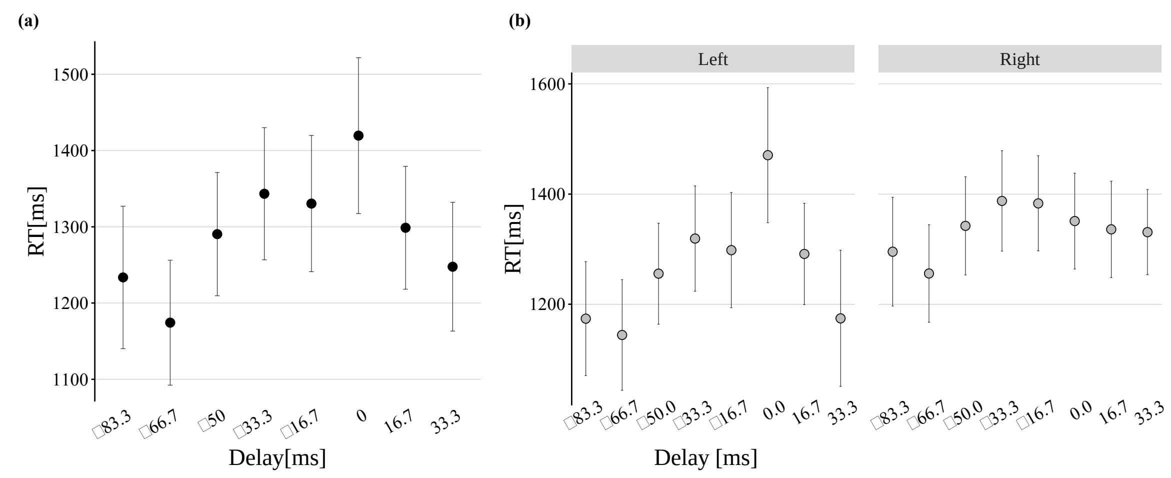


***Figure 5*. Response times**. (a) Averaged RTs for all participants. (b) Averaged RTs for LVF*(Left) and RVF (Right).*

The outcome of the second repeated measures ANOVAs of the RTs (Table 3) with Visual Field as the between-subject factor and Response Time as the within-subject factor, revealed non-significant effect of Response Time [F (1, 24) = .898, p = .35]. However, results [F (7,168) = 2,326, p = .02] showed a significant mean difference between the visual fields (see ***Figure 6***), indicating that participants responded faster in the LVF condition.

ANOVA Table for Response Time

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Subject	24	45878936,658	1911622,361				
Visual Field	1	362820,883	362820,883	,898	,3528	,898	,142
Visual Field * Subject	24	9700183,261	404174,303				
Lag	7	1752959,086	250422,727	6,528	<,0001	45,698	1,000
Lag * Subject	168	6444412,145	38359,596				
Visual Field * Lag	7	686080,535	98011,505	2,326	,0273	16,282	,842
Visual Field * Lag * Subject	168	7079115,195	42137,590				

Means Table for Response Time
Effect: Visual Field * Lag

	Count	Mean	Std. Dev.	Std. Err.
LVF, -83	25	1167,750	475,399	95,080
LVF, -66	25	1150,202	462,040	92,408
LVF, -50	25	1266,845	421,899	84,380
LVF, -33	25	1342,211	442,244	88,449
LVF, -16	25	1286,412	472,331	94,466
LVF, 00	25	1469,617	566,002	113,200
LVF, +16	25	1320,948	440,518	88,104
LVF, +33	25	1166,065	566,239	113,248
RVF, -83	25	1281,042	400,688	80,138
RVF, -66	25	1252,839	353,176	70,635
RVF, -50	25	1341,567	353,720	70,744
RVF, -33	25	1381,269	366,252	73,250
RVF, -16	25	1374,862	346,574	69,315
RVF, 00	25	1354,147	346,447	69,289
RVF, +16	25	1320,478	355,585	71,117
RVF, +33	25	1345,722	311,374	62,275

Table 3. ANOVAs of the RTs with imputation

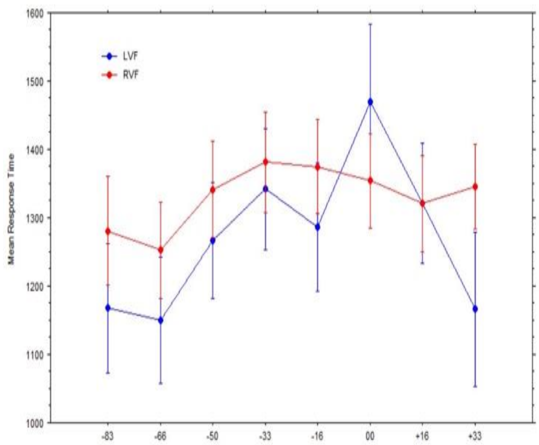


Figure 6. RTs means plot

4.2.3 Pupillary responses.

A repeated-measures ANOVA of the pupil change with Lag as the within subject factor and Pupil Change as between subject factor (Table 3) revealed a significant effect of Lag [F (7, 168) = 2,63, p = .013]. Indicating that participants were more engaged with attention (i.e., larger pupils) on the LVF compare to RVF (see ***Figure*** 7). However, the average pupil changes of two factor ANOVA with Lag and Visual Field as within subject factor and pupil change as between subject factor did not show a significant effect of Lag in different visual fields [F (7,168) = 1.18, p = .313].

ANOVA Table for Pupil Change

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Subject	24	,809	,034				
Visual Field	1	,006	,006	,749	,3955	,749	,127
Visual Field * Subject	24	,199	,008				
Lag	7	,050	,007	2,635	,0131	18,448	,894
Lag * Subject	168	,454	,003				
Visual Field * Lag	7	,021	,003	1,186	,3135	8,301	,494
Visual Field * Lag * Subject	168	,421	,003				

Means Table for Pupil Change
Effect: Visual Field * Lag

	Count	Mean	Std. Dev.	Std. Err.
LVF, -83	25	,035	,067	,013
LVF, -66	25	,070	,072	,014
LVF, -50	25	,052	,053	,011
LVF, -33	25	,058	,073	,015
LVF, -16	25	,073	,091	,018
LVF, 00	25	,060	,063	,013
LVF, +16	25	,033	,066	,013
LVF, +33	25	,042	,082	,016
RVF, -83	25	,031	,085	,017
RVF, -66	25	,045	,065	,013
RVF, -50	25	,034	,073	,015
RVF, -33	25	,059	,068	,014
RVF, -16	25	,066	,061	,012
RVF, 00	25	,034	,063	,013
RVF, +16	25	,054	,060	,012
RVF, +33	25	,037	,068	,014

Table 4. ANOVA of pupil change with imputation

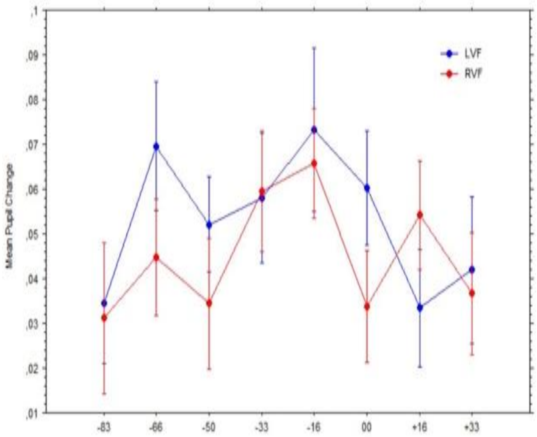


Figure 7. Pupil change means plot

Moreover, ***Figure 8(a)*** shows the time course of pupillary changes from prior and posterior to the stimulus onset from -500ms to 2000ms relative to the averaged pupil size in baseline period. The averaged pupil changes were averaged from the presentation period of stimulus onset until 1,000 ms as shown in ***Figure 8(b).*** We tested second-order polynomials fitting (i.e., $a \neq 0$) as Equation (1) and monotonic fitting (i.e., $a = 0$) as Equation (2) to the relationships between Delay and pupil size using a least squares method. The estimated a was significant (estimated *a*= -6.3622031^{-6}, t = -1.8746793, p = 0.0623168, b = -3.3134719^{-4}, t = -1.6251264, p = 0.1057344) indicating that the second-order polynomials explained well the relationship between Delay and pupil size compared to the monotonic fitting. ***Figure 8(c), (d)*** showed the same analysis as above in each visual field.

$$y = ax^2 + bx + c - (1)$$

$$y = bx + c - (2)$$

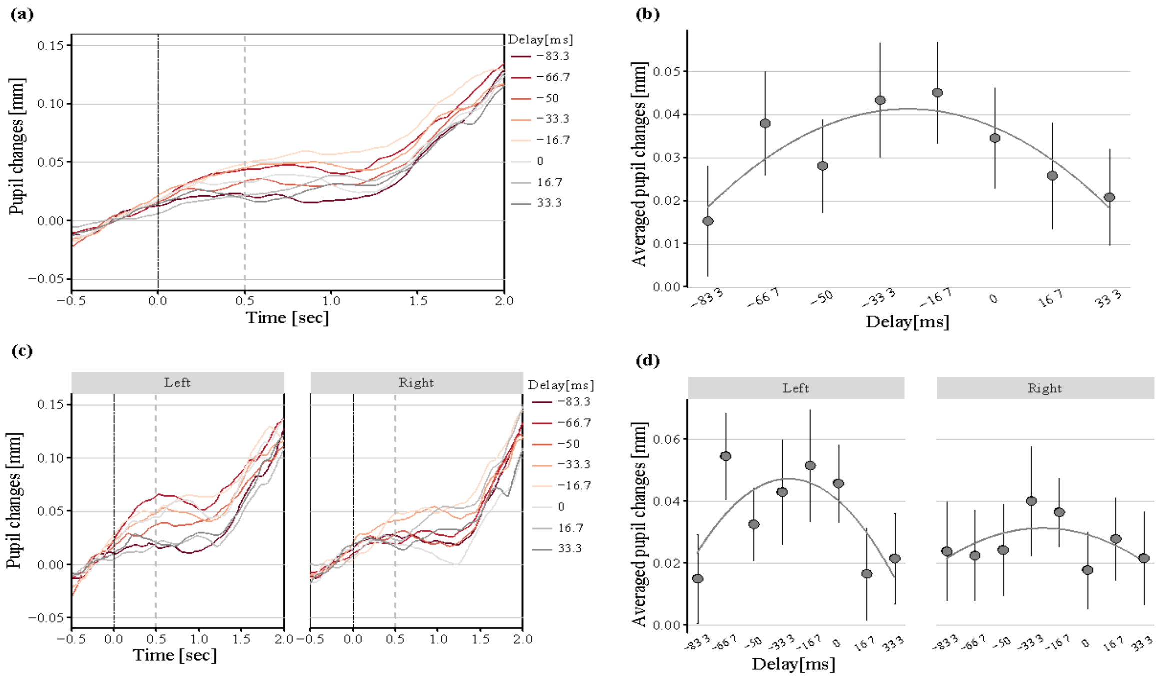


Figure 8. Pupillary diameter changes over time and delays. **(a)** Pupil change diameter for all participants. **(b)** Averaged psychometric curve for all participants. **(c)** Pupil change diameter for LVF (Left) and RVF (Right). **(d)** Averaged psychometric curve for LVF (Left) and RVF (Right).

5. Discussion

Specifically, this thesis had three main purposes: 1) To study how visual processing deals with motion interpolation. 2) To investigate whether pupillary responses and eye movements can index mental effort during FLE task. 3) To investigate or confirm functional asymmetries (e.g., Strong et al., 2019) across left and right visual fields in terms of motion stimuli processing.

Our FLE experiment results with the focus of visual fields using pupillary responses as an online measure of attention yielded significant evidence for almost all of the main purposes.

5.1 Visual Field Asymmetries

One of the main objectives of this thesis was to investigate functional asymmetries across visual fields. All statistical analysis results measuring Accuracy/performance, Lag effect showed significant difference across visual fields since it nearly reached a significant advantage in the LVF than in RVF, which brings some support to the idea of a superiority of the LVF confirming *Hypothesis 1*. Results were consistent also with previous studies (e.g., Kanai et al, 2014; Bosworth et al., 2011) indicating that there were asymmetries across visual fields reflecting motion interpolation. Based on the previous studies it is known that LVF is more vulnerable to the attentional processes, especially the clinical literature showed ample evidence (e.g., parietal damage patients generally have hemineglect of the LVF: Brain, 1941; Costa et al., 1969; Heilman & Van Den Abell, 1980). Different excitation of subdivisions in MT V5 / MT + along the two hemispheres might explain this known asymmetry (Strong et al., 2019). MT / TO-1 and MST / TO-2 are the two major subdivisions of MTV5 / MT +. The second region includes neurons with strong receptive fields that range from the previous one to the 15 ° ipsilateral hemifield (Strong et al., 2017). As a result, Strong et al., (2019) discovered that right MThV5/MT + has an enhanced role in the processing of translational motion across the entire visual field.

Consistently, Boulinguez, Ferrois, and Grumer (2003) reported right hemisphere bias for motion perception. Their reaction time experiments revealed that trajectory perception and estimation can be accessed and analysed more quickly in the right hemisphere. Additionally, ffytche et al., (2000) investigated visual evoked potentials (VEPs) generated by motion stimuli in hV5/ MT + across the right and left cerebral hemispheres and they found that when stimuli were viewed ipsilaterally, the VEP displayed a delay compared to contra-lateral stimulation. The ipsilateral delay in the left hemisphere was 11 milliseconds, although it was just 3 milliseconds in the right hemisphere.

5.2 Pupillary Findings and Mental-Effort

Another main objective of this project was to investigate whether pupillary responses and eye movements can index mental effort during the FLE task. Results showed that pupillary responses can index mental effort; participants had a tendency to larger pupils in the LVF compared to RVF, which is consistent with *Hypothesis 2*, although it failed to reach significance. Furthermore, this finding is a novel finding compare to other studies.

In natural environments, the pupil is mostly driven by the luminance (and presumably colour and contrast) at the gazed spot, although it is often regulated by attention and cognitive factors (Ajasse et al., 2018). A possible explanation for different pupillary dilations when viewing moving and flashed object at different lags can be that the phasic mode of activity in the locus coeruleus (LC) is more engaged at a particular lag than others. A look at ***Figure 8*** suggests that the pupil, therefore mental effort, was greater around the lag corresponding to the PSE, i.e., about -33 ms, suggesting that the lag corresponding to the percept of simultaneity recruited more cognitive resources. Recent neuroscience studies have also confirmed that the pupil represents the activity of LC that is the nucleus of the norepinephrine system in the brain. Thus, several studies showed that pupillary changes are a reliable index of mental effort and the intensity of attentional mechanisms (Kahneman, 1973; Wilhelm et al., 1999; Laeng et al., 2012).

The relation between the FLE and attention is noteworthy. The amount of attention dedicated to the stimulus is considered to affect the degree of FLE (Sarich et al., 2007; Shioiri et al., 2010), and also the predictability of the stimulus (Baldo & Namba, 2002; Namba & Baldo, 2004; Vreven & Verghese, 2005). According to some research, the FLE could be interpreted in terms of attention (Baldo et al., 2002; Khurana et al., 2000). The result of the present study can be considered as yet another example of psychophysical evidence demonstrating an association between attention and the FLE. Pupil responses are a prominent eye movement. Like other types of eye movements such as smooth pursuit and saccades, they have both reflexive and voluntary actions (Mathot, 2018). According to Kahneman (1973) phasic pupillary responses reflect the intensive aspect of attention, thus in this study pupillometry was used to measure pupil dilation in terms of attention during the whole experiment. Albeit there is still a lot to learn about the role of pupil responses, they are undeniably important in active vision.

Previous studies (Alvarez & Cavanagh, 2005; Chakravarthi & Cavanagh, 2009; Shipp, 2011) showed attention to LVF requires different neural resources than RVF and this difference become more prominent on time-sensitive attentional tasks (Mathews & Welch, 2015), thus lastly, we hypothesized that perceptual judgement should be less affected by visual illusion on the LVF (i.e., accuracy/performance will be better) compare to the RVF. Results showed a trend towards a difference between the visual fields, indicating that participants respond faster in the LVF condition, consistent with *Hypothesis 3*. RTs were longest at the zero point; this effect was mainly due to the long RTs for the LVF. This indicates that physical simultaneity required extra processing, more than during delays. Furthermore, -33 delay occurred in both measurements (RTs for LVF and RVF), and this is the delay that corresponds to subjective simultaneity for PSE. Indeed, this is consistent with flash-lag effects seen in previously mentioned studies (see, e.g., Kanai et al., 2014; Matthews & Welch, 2015). Moreover, results were consistent with the divided visual field paradigm showing functional advantages for a visual field in a specific task (Banich, 2003; Bourne, 2006).

According to Wardle (1998) response time delay is caused by two factors. The first is the time it takes for photons to reach the retina for the individual to perceive a light (i.e., the time delay in human vision). The second factor is the interval between nerve impulses leaving the brain and muscle movement. For this study, RTs were calculated from the time of stimulus offset to the participants' key presses, and results provide a visual field and lag interaction for response time: participants were more accurate, and faster.

Further, Khurana, Watanabe and Nijhawan's (2000) study showed that both the 'lag correction (where the brain uses more recent retinal input to modify the position of previously identified objects) of moving objects and registration of flashing objects are caused by neuronal transmission delays rather than attentional delays. Hence, they claimed that the FLE is not affected by attentional deployment. Contrary to this view trended results in our study showed that participants are more engaged with attention (i.e., larger pupils) in the LVF.

5.3 General Discussion

Most of the existing FLE theories argue that the position of the moving object cannot be encoded correctly when a temporally brief flash is used as a temporal marker. For example, according to motion extrapolation theory, the position of the constantly visible moving ring could be extrapolated forward in time, whereas there is no corresponding compensation mechanism for the suddenly appearing flashed object. According to the "postdiction" theory, the position of a moving object is often an average value of positions sampled over a longer time period. These motion integration processes are reset by the flash, so only positions after the time of the flash are used to calculate the location of the moving object. As a result, the moving object's position seems to have shifted forward within the direction of motion (see, e.g., Eagleman & Sejnowski, 2000). Another account of the FLE, the differential latency theory, claim that perception of the flash is delayed due to longer perceptual processing times. As a result, when the flash is perceived, the moving stimulus has already moved forward to its next location, which accounts for the FLE (see, e.g., Purushothaman et al., 1998; Whitney & Murakami, 1998).

Additionally, single-cell recordings from the ganglion cells in the retinae of a rabbit and a salamander revealed that moving stimuli cause a neuronal activation wave that is passing forward the trajectory of motion, as extrapolation theory predicted (Berry et al., 1999). Although it is obvious that neuronal processing delays of moving stimuli are compensated by retinal extrapolation systems (Berry et al., 1999). On the other hand, some psychophysical findings indeed pointed FLE to a higher-level cortical origin: the FLE observed when the observer is accelerated himself on a rotating chair (Schlag et al., 2000), which is indicating that the FLE could be seen even when there is no retinal motion.

An extrapolation mechanism, which would adjust the position of the object representation based on a predicted trajectory, is suggested to explain the flash-lag effect (Nijhawan,1994). Nevertheless, the current project and other previous research showed that an interpolation mechanism, which retroactively 'fill in' the trajectory of the object when it is known where the object is heading, also underlies the FLE (Hogendoorn et al., 2008). Hence, a retinal extrapolation process cannot completely explain the FLE: Higher-level cortical mechanisms seem to be needed to understand the FLE (Niemann et al., 2006). We, therefore, measured pupil responses and studied different visual fields for the present FLE study to contribute the phenomenon.

It is obvious that the FLE is not caused by an inability to accurately integrate position information of the moving object with temporal information from a short-lived flash that appears momentarily. Even though, nearly all existing flash-lag effect accounts support the idea that information integration processes error is responsible for the FLE, there are other exceptional accounts that rule out this idea, for instance, attention account.

After more than a century of research on visual attention, it's clear that various dimensions of visual analysis are influenced by attention. To date, however, the empirical enterprise dedicated to understanding attentional phenomena has mostly concentrated on how attention influences visual performance (e.g., speed or accuracy), instead of addressing whether attention can shape the phenomenological appearance of visual objects. After all, the effects of attention on visual performance have been reported in terms of accuracy (e.g., Bashinski & Bacharach, 1980; Lyon, 1990), and response times (e.g., Posner, 1980). Whereas there is no doubt that attention enhances visual analysis power, nevertheless, it is unclear if attention often affects the phenomenological appearance of visual stimulus (Yeshurun & Carrasco, 1998). According to attention shift theory (see, e.g., Baldo & Klein, 1995), the moving object is displaced when the flash inevitably attracts the observer's attention to its location, thus the attention needs to be redirected to the moving object during a time-consuming process (Baldo & Klein, 1995; Baldo et al., 2002). The attention account claims that delays in processing the location of a moving object are generated not only by intrusion in estimating the position of the moving and the flashed object, as well as by the need to distribute attention first to the flash, then to the moving object. Yet, based on the literature we are well-aware that attention can only modulate the flash-lag effect; it cannot account for the illusion entirely. Besides that, several studies failed to provide significant effects of attention on the FLE (Khurana & Nijhawan, 1995; Khurana et al., 2000).

5.4 Limitations

Despite the many advantages of the present study (a solid experimental design and significant novel findings compared to other studies); it obviously had several limitations.

First and foremost, the small sample size was an important limitation to current study, in the beginning we plan to recruit data from at least 30 participants, but because of the COVID-19 pandemic we had to stop testing at 27. Furthermore, we lost some data's during statistical analysis; Two participants in left visual field condition and four participants in right visual field condition were excluded from pupil analyses because the rejected trials were more than 50% of whole trials.

Another limitation was that we investigated FLE only unimodally, we only measured visual attention, however several studies showed that auditory attention is also crucial on studying FLE effect, therefore a cross-modal version could perform to see audio-visual interactions in FLE.

5.5 Future Implications

Many theories of the flash-lag effect tried to explain the phenomenon such as, motion extrapolation (Nijhawan, 1994), motion interpolation (Hogendoorn et al., 2008) attention (Baldo & Klein, 1995), and "postdiction" (Eagleman & Sejnowski, 2000). Whatever the explanation for FLE, an intriguing question is if the phenomenon is exclusive to visual stimuli or whether it also happens in other senses and cross-modally, and whether these effects can be accurately related to neuronal latencies. However, this thesis project was done unimodally, we studied FLE only in vision. Literature showed that the flash-lag effect is not peculiar to vision, but occurs in audition, and also cross-modally. The results of Burr and Alais (2006) suggested that vision and audition have their own attentional resources. Attention is not a unified phenomenon, but rather occurs at several cortical stages, namely early sensory processing and the primary cortical regions of V1 and A1 (Kanwisher & Wojciulik, 2000). To our knowledge, it is the first study that investigating FLE in terms of pupil dilation (i.e., using pupillometry). Thus, in order to strengthen the significant findings found in this study, future studies that aim to investigate FLE in terms of mental effort (i.e., attention) could study FLE cross-modally.

5.6 Conclusion

The present study can be concluded that it provides the first empirical evidence about the effects of flash-lag on pupillary responses. The trended results in this study revealed that the effects of visual attention reflecting motion interpolation are larger in the LVF than in the RVF, despite the precise nature of hemifields' attentional asymmetry. Although it is challenging to separate these two possibilities, clinical and brain imaging studies have precisely determined the effect of attention in the right hemisphere. Moreover, we found that performance/accuracy is better on LVF. Such findings indicate that attention-based increases in neural responses are higher in the right hemisphere than in the left, specifically in the dorsal stream (Righi & Vettel, 2011). Ultimately, results provide a visual field and lag interaction for response time: participants were more accurate, and faster.

Declaration of Contribution

The planning and the design of the present research was done by my supervisor. Although the written master's thesis is my own work, I preferred to use the pronoun "we" to preserve the integrity of the meaning.

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Appendix

Instruction