THE EFFECTS OF MOTION AND SMOOTH PURSUIT EYE MOVEMENTS ON THE VISIBILITY OF CHROMATIC STIMULI

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DECLARATION OF ORIGINALITY

I, Dilce Tanrıverdi, certify that

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ABSTRACT

The Effects of Motion and Smooth Pursuit Eye Movements on the Visibility of Chromatic Stimuli

Previous literature showed that a drifting inducer modulates the sensitivity of an achromatic target abutting the inducer when the eyes are steady. Additionally, it has been shown that the contrast sensitivity to stimuli changes during smooth pursuit eye movements. Here, we investigated the changes in chromatic contrast sensitivity during the smooth pursuit for abutting target gratings. In the first experiment, we established the changes in chromatic contrast sensitivity caused by the inducer’s motion during fixation. Experiment 2 established the modulation of chromatic contrast sensitivity during smooth pursuit for the isolated dynamic target gratings. Finally, Experiments 3A and 3B investigated the changes in chromatic contrast sensitivity caused by the inducer’s motion during smooth pursuit. Additionally, by using isoluminant and luminance-modulated chromatic gratings, all experiments investigated the interaction of chromatic and luminance signals to better understand where the observed effects are processed in the brain. The contrast sensitivity was measured with a 2AFC task using the method of constant stimuli. Observers reported whether a low contrast target grating appeared above or below the fixation point. Results revealed a phase-dependent motion-induced sensitivity modulation during fixation, a directional selective contrast sensitivity modulation for dynamic target gratings during the pursuit, and an interaction between motion direction and smooth pursuit for abutting dynamic gratings. The results are discussed in terms of the interaction between chromatic motion perception and smooth pursuit. Moreover, the potential neural substrates of this interaction are discussed.

ÖZET

Yavaş İzleme Göz Takip Hareketinin ve Hareket Algısının Kromatik Uyaranların Görünürlüğü Üzerindeki Etkileri

Gözler sabitken ekranda gösterilen akromatik bir uyaranın hareketi, o uyarana bitişik hedef objenin görünürlüğünü etkilemektedir. Ek olarak, kromatik kontrast duyarlılığının, yavaş izleme göz takip hareketleri sırasında değiştiği de bilinmektedir. Bu tezde, hareketli bir ızgara uyaranına bitişik kromatik hedef ızgara uyaranlarının görünürlüklerinin göz hareketleri sırasındaki değişimi incelenmiştir. İlk deneyde, sabit göz konumu sırasında nesnenin hareketinden kaynaklanan kromatik kontrast duyarlılığındaki değişiklikler belirlenmiştir. Deney 2, ekranda tek başına sunulan dinamik hedef ızgara uyaranları için göz takibi sırasında kromatik kontrast duyarlılığının modülasyonunu ortaya sermiştir. Son olarak, Deney 3A ve 3B'de, göz hareketleri sırasında bitişik nesnenin hareketinin hedef uyaran üzerinde neden olduğu kontrast duyarlılığındaki değişiklikleri araştırılmıştır. Ek olarak, dört deneyde de gözlenen etkilerin beyinde nerede işlendiğini anlamak için kromatik ve lüminans sinyallerinin etkileşimlerine bakılmıştır. Kontrast duyarlılığı, sabit uyaran yöntemi kullanılarak 2AFC görevi ile ölçülmüştür. Deneyler sırasında gözlemciler, düşük kontrastlı hedef uyaranın sabitleme noktasının üstünde mi yoksa altında mı belirdiğini bildirmişlerdir. Sonuçlar, sabit göz pozisyonu sırasında faza ve harekete bağlı bir duyarlılık modülasyonu, göz takibi sırasında dinamik hedef ızgaralar için hareket yönüne bağlı bir duyarlılık modülasyonu ve bitişik dinamik ızgara uyaranları için hareket yönü ve göz hareketleri arasında bir etkileşim ortaya çıkarmıştır. Sonuçlar, kromatik hareket algısı ve göz hareketleri arasındaki etkileşim açısından ve dahası, bu etkileşimin potansiyel nöral substratları bağlamında tartışılmıştır.

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DEDICATION

To my mom and dad,

Thank you for always allowing me to chase after my dreams.

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CHAPTER 1

INTRODUCTION

Most of our current knowledge about the visual system was derived from studies, where isolated simple stimuli were observed while eyes had been fixed. In the real world, on the other hand, the visual system is concerned with solving the spatio-temporal relationships across several edges, surfaces, textures, and object boundaries within the context of self-produced information from motor actions, such as eye movements (Gibson, 1979). It is known that the visibility of a certain target can be affected by the contextual influences of various spatial features, including both static and dynamic surrounding stimuli (Levitt & Lund, 1997). The presence of visual stimuli placed nearby a target stimulus is known to exert both facilitative (Snowden & Hammett, 1998) or suppressive (Polat & Sagi, 1993) modulatory effects. Similar suppressive and excitatory modulatory effects have also been demonstrated during the self-initiated eye movements (Schütz, Braun & Gegenfurtner, 2007a; Schütz, Braun, Kerzel, & Gegenfurtner, 2008).

This thesis is mainly motivated by two lines of research: (1) the study conducted by Roach, McGraw, and Johnston (2011), where they demonstrated the influence of contextual effects of surround motion on the visibility of a low contrast target stimulus and (2) the work by Schütz, et al. (2008), where they observed a facilitative effect of smooth pursuit eye movements on the visibility of isoluminant chromatic stimuli. Here, we combine these two paradigms to investigate the contextual influences of object motion, smooth pursuit eye movements, and their interaction on the chromatic contrast sensitivity. Additionally, we aim at looking at the interaction between the effects of chromatic and luminance signals on contrast sensitivity for dynamic stimulus during the smooth pursuit to better understand the role of the parvocellular pathway on motion perception and pursuit execution. More specifically, as a first experiment, we investigate the visibility of abutted spatio-temporal patterns using isoluminant and luminance-modulated chromatic gratings (Experiment 1). In the second experiment, we investigate the visibility of dynamic isoluminant and luminance-modulated chromatic target gratings during smooth pursuit eye movements (Experiment 2). The third experiment is set to investigate the visibility of abutted spatio-temporal isoluminant and luminance-modulated chromatic gratings during smooth pursuit eye movements (Experiments 3A and 3B). Within this context, in the Introduction, I will first describe the literature on contrast sensitivity, motion perception, smooth pursuit eye movements, and their interactions. Then, I will introduce the novelty which the thesis offers to the literature.

1.1 Contrast sensitivity

Contrast sensitivity is the ability of observers to detect low-contrast visual patterns. These visual patterns can be modulated by either luminance or hue without any change of luminance (isoluminance). The contrast sensitivity function (CSF) is used to derive the visual system’s acuity to any pattern. It has been shown that both the spatial and the temporal CSF functions for color differ from those for luminance (for a comprehensive review, Lee, 2019).

Chromatic and luminance contrast sensitivities differ in many characteristics. Luminance sensitivity, especially for sinewave gratings, is usually defined by Michelson contrast which is the difference between the highest and lowest luminance value divided by their sum (Michelson, 1995). Temporal CSF for achromatic stimuli reveals a band-pass shape and its detectability peaks at around 10 Hz (de Lange, 1958). Spatial CSF, on the other hand, reveals a peak at 1 cpd with a low-pass shape (Campbell & Robson, 1968). The magnocellular pathway, starting from the parasol cells from the retina towards the magnocellular layers of the lateral geniculate nucleus contains cells that are sensitive to changes in luminance (Lee, Sun & Valberg, 2011). These cells have similar response characteristics to temporal CSFs for achromatic stimuli (Lee, 2019). Spatial substrates of achromatic CSF seem to be shared by both magnocellular and parvocellular pathways (Lee, 2019). While the sensitivity of magnocellular pathway cells is higher for low spatial frequency signals, the sensitivity of parvocellular pathway cells is higher for high spatial frequency signals (Derrington & Lennie, 1984).

Chromatic contrast sensitivity is harder to define. The response to a chromatic stimulus depends on the wavelength of light sources in relation to the visual pigments' absorption, which overlaps for the medium-wavelength- (M) and long-wavelength-sensitive-cones (L) on the retina. Because of this overlap, chromatic contrast is limited for the magenta-cyan axis. Calculation of Michelson contrast for the medium- and long-wavelength modulation is executed using each cone and cone contrast value (Lee, 2019). Contrary to the achromatic CSF, chromatic temporal CSF reveals a low-pass shape, where the highest contrast sensitivity could be observed at around 0.6 Hz (McKeefry, Murray, & Kulikowski, 2001). Starting from the midget cells from the retina, the parvocellular pathway responds to the L-M modulation in a low pass-shape (Lee, Shapley, Hawken, & Sun, 2012). The spatial CSF for the purely chromatic signal has a low pass shape (Kim, Mantiuk, & Lee, 2013). Thus, parvocellular cells provide the neural substrate for the spatial mechanism underlying the L-M signals.

Contrast sensitivity can be affected by the characteristics of the objects nearby the target (Arnold, Thompson, and Johnston, 2007; Polat & Sagi, 1993; Snowden & Hammett, 1998) or oculomotor changes during the detection processes (Burr, Morrone, & Ross, 1994; Schütz et al., 2008), which will be discussed in more detail in the incoming parts.

1.2 Contextual effects for static stimuli on contrast sensitivity

For static stimuli, the presence of objects presented nearby a target stimulus can exert both suppressive and facilitative effects on the target's visibility (Snowden & Hammett, 1998; Polat & Sagi, 1993). The suppression of the contrast sensitivity by a nearby object is called surround suppression. Both physiological and psychophysical studies showed that if another stimulus surrounds a target stimulus, the target's visibility gets suppressed (Knierim & Van Essen, 1992; Snowden & Hammett, 1998). Surround suppression has been observed on the neurons of area V1 of macaque monkeys for achromatic stimuli (Knierim & Van Essen, 1992). Several different studies examined the tuning properties of the surround suppression. Psychophysical studies showed that surround suppression is highest when the surround contrast is higher than the target contrast (Xing & Heeger, 2001), the target and the surround are iso-oriented and both have the same spatial frequency (Petrov, Carandini, & McKee, 2005; Serrano-Pedraza, Grady, & Read, 2012). The suppression has been demonstrated to be weaker when the distance between the target and the surrounding stimuli is larger and the spatial extent of the surrounding stimuli is small (Cannon & Fullenkamp, 1991). The examination of the phase dependence of surround suppression has led to some conflicting results. While some studies showed the modulation of the phase difference between center and surround stimuli (Ejima & Takahashi, 1985; Olzak & Laurinen, 1999; Yu, Klein, & Levi, 2001), others failed to observe such modulation (Petrov and McKee, 2006; Xing and Heeger, 2001).

All these studies investigated the surrounding suppression effect using achromatic stimuli. Physiological evidence, however, shows that surround suppression can also occur for chromatic isoluminant stimuli (Livingstone and Hubel, 1984; Michael, 1978; Ts'o and Gilbert, 1988). In addition to the evidence for surround suppression using chromatic stimuli, Wachtler, Sejnowski, and Albright (2003) also demonstrated that, depending on the chromatic relationship between the target and the background, there might be facilitation as well as suppression in the response of neurons in area V1 by surrounding chromatic stimuli. Solomon, Peirce, & Lennie (2003), on the other hand, failed to observe an alteration of the chromatic tuning of the classical receptive fields in areas V1 and V2 by the surrounding context. They attributed the difference of their results from those of Wachtler et al. to the conscious states of the animals during the recordings (whereas awake monkeys were used for Wachtler et al. (2003), Solomon et al. (2003) had used anesthetized monkeys) and relatively large receptive fields used by Wachtler et al. (2003). Solomon et al. suggested that the contextual effects observed by Wachtler et al. could be a result of feedback from the higher-level areas, rather than originating from the primary visual cortex.

In addition to the suppressive effects, the presence of a nearby stimulus can also increase the visibility of a target object under certain conditions. This facilitation effect is called flank facilitation. Flank facilitation is an increase in the contrast sensitivity caused by the presentation of a Gabor between two collinear Gabor patches (Polat & Sagi, 1993; 1994). Psychophysical studies demonstrated that for facilitation to occur, the distance between the flanking and the target stimuli must be sufficient (Polat & Sagi, 1993). The collinear property of the bars is also important such that when the Gabor patches are presented in parallel to each other, the degree of facilitation decreases (Polat & Sagi, 1994). Changes in the relative properties of the target and flanker stimulus, such as variations in orientation or spatial frequency, often minimize facilitation (Chen & Tyler, 2002; Polat & Sagi, 1993). Notably, the relative phase of the flankers and the target Gabor patches are also important for flank facilitation. It is known that when the phase of the flanking stimuli is opposite to that of the target, the facilitation is significantly reduced (Solomon, Watson, & Morgan, 1999).

Flank facilitation occurs for both achromatic and chromatic stimuli (Huang, Mullen, & Hess, 2007). Huang et al. (2007) showed that the degree of facilitation is the same for chromatic stimuli and achromatic stimuli. They also showed that facilitation does not occur across achromatic and chromatic stimuli. In line with the studies using achromatic stimuli, Huang et al. demonstrated that when the phases of the sinewaves of target and flanker gratings are congruent, the facilitation increases for the isoluminant stimuli. However, unlike achromatic stimuli, a suppression effect is observed in the incongruent phase condition when the target and flankers are spatially close to each other (2.7° visual angel compared to 4° and 8°) in the spatial space.

Although we aim to investigate the contextual effects of motion on the visibility of chromatic stimulus, these studies show that the sole spatial presence of a nearby stimulus can also affect the contrast sensitivity of the system to the target object. Therefore, in the incoming chapters, I will discuss whether the results we present are motion-specific or caused by spatial context effects.

1.3 Motion perception and contrast sensitivity

Motion perception refers to the process of inferring the speed and position of elements in a scene from the visual input. Many of the receptive fields in V1 are direction and orientation-selective (Hubel & Weisel, 1968). Therefore, the motion information can be detected by integrating the outputs of V1cells with different orientation preferences and spatio-temporal characteristics (Adelson & Bergen, 1985). Furthermore, extrastriate cortical areas such as V3A and MT respond to the global motion by integrating the local motion signals from V1 (Braddick et al., 2001; Cowey, Campana, Walsh, & Vaina 2006).

For dynamic stimuli, the presence of surrounding stimuli affects the performance for motion discrimination. Tadin, Lappin, Gilroy, and Blake (2003) reported that, as the size of a high contrast stimulus increases, observers become worse at discriminating the direction of motion, whereas at low contrast, increasing the stimulus size improves performance. Tadin et al. (2003) hypothesized that this effect, called spatial suppression, results from center-surround antagonism in motion-selective neurons in the cortical visual region area MT. Conversely, Chen (2011) argued that spatial suppression is a product of center-surround antagonism, but it does not occur from the inhibition observed in the cells of area MT. Rather, spatial suppression of motion occurs via integrating the neurons’ center-surround antagonistic responses in area V1 by MT.

In the absence of eye movement, during steady eye conditions, motion inside of a static envelope can modulate the visibility of a low contrast target abutting the high contrast target. Arnold, Thompson, and Johnston (2007) came up with a paradigm where the motion direction of the high contrast stimulus (inducer) provides a template for the relative position of the low contrast stimulus (target). According to this configuration, the target's position is defined by the drift direction of the inducer grating. The target can either be in the leading or in the trailing position relative to the inducer grating. With this paradigm, Arnold et al. showed that when the target was in the leading position, the target's visibility was higher than when the target was in the trailing position. Using the same paradigm, Roach et al. (2011) discovered that the phase of the inducer and target sinewave gratings modulate the visibility of the target in the leading position. Accordingly, if the phases of target and inducer gratings were congruent with each other, the target's visibility in the leading position was higher than the condition where the phases of the target and inducer gratings were incongruent with each other. They explained their results within the context of a forward prediction model. According to this model, the target's visual input gets paired with an internal prediction based on prior. If the prior matches with the visual signal (congruent phase), it assists the detection of the target. On the other hand, if the internal prediction and visual signal do not match, the target's visibility is distrupted. This account is supported by previous research showing that the motion signals are integrated along the motion trajectory that increases the visual system's sensitivity for the stimuli moving along a predictable trajectory (Grzywacz, Watamaniuk, & McKee, 1995). A continuous motion trajectory is thought to induce a facilitative flow of activity in similarly tuned motion detectors, predicting the path of the inducing motion (Verghese & McKee, 2002).

Arnold, Marinovic, and Whitney (2014), on the other hand, using the same paradigm, suggested a non-predictive mechanism. They showed that the phase modulation in the leading edge of the motion also occurs in the trailing edge, yet in a smaller magnitude. Additionally, they also showed the modulation effects on the adjacent edge of the inducer. Moreover, they reported the modulation using flickering stimuli without a detectible motion direction, demonstrating that the mechanism underlying the modulations in the contrast sensitivity is not necessarily linked to motion. From these findings, they argued that the phase modulation results from a phase-sensitive spatial summation mechanism where the summation of the physical input spread across the retina. They also argued that this spatial summation mechanism is attenuated by the motion blur mechanisms at the trailing edge of the motion, explaining the reduction in the magnitude of the effect on the trailing end.

1.4 Chromatic motion perception and contrast sensitivity

Many early theories of vision suggested that the visual system has parallel and separate streams of image processing (Mishkin & Ungerleider, 1982). According to these theories, the magnocellular pathway receives mostly achromatic, transient signals and feeds information into the dorsal pathway (Hawken, Parker & Lund, 1988). The dorsal pathway is concerned with processing motion and spatial position (Zeki, 1974). On the other hand, the parvocellular pathway mainly receives sustained and chromatic signals and feeds this information to the ventral pathway (Maunsell & Newsome, 1987). The ventral pathway is concerned with processing color (Zeki, 1971) and form (Hanazawa & Komatsu, 2001).

Although the above theories suggest that motion and color information is processed in different pathways, the most recent literature shows that there is an interaction between the two. Motion information can be extracted from a signal modulated only via chromatic input, in other words, from isoluminant signals. (for review, Cropper & Wuerger, 2005; Gegenfurtner & Hawken, 1996). When a stimulus is defined as chromatic, its essential properties that enable its detection are coded only by a change in the stimulus hue rather than luminance. This stimulus property is referred to as isoluminance. However, even when a magenta-cyan chromatic stimulus is presented at physical isoluminance, chromatic aberration on the retina can cause a shift from perfect isoluminance under some conditions (Howarth & Bradley, 1986). This shift typically occurs for stimuli with a spatial frequency higher than 1 cpd at high temporal frequencies (Cropper & Wuerger, 2005) and can be accounted for using several behavioral methods such as minimally distinct border (Boynton, 1979) and minimum motion (Anstis & Cavangh, 1983).

Properties of isoluminant motion are different from those of achromatic motion. The movement of isoluminant stimuli appears to be slower than that of luminance stimuli (Cavanagh, Tyler, & Favreau, 1984). Additionally, the detection/direction threshold ratio for the isoluminant motion is higher than the ratio for the luminance motion (Cropper & Derrington, 1994). These differences between the isoluminance and luminance-based motion led to theories that two different motion streams process different motion signals (Cropper & Wuerger, 2005; Gegenfurtner & Hawken, 1996). Gegenfurtner and Hawken (1996) suggested that these two different motion streams differ from each other in terms of their temporal properties. Although neither of the streams are color-blind, the fast stream is mainly concerned with the velocity of the motion, and the other one is highly sensitive to color. On the other hand, Cropper and Wuerger (2005) suggested that these two streams differ in spatial and temporal characteristics. They also suggested that purely chromatic motion is confined to the limits of the fovea.

The underlying neural substrates for the isoluminant motion are still argued. Gegenfurtner and Hawken (1996), using data from patients suffering from cerebral akinetopsia, suggested that the neural substrates for isoluminant motion could be a pathway between V3 and V4. On the other hand, Cropper and Wuerger (2005) suggested that in the lack of luminance signals, neurons in MT could be responsible for the processing of isoluminant motion with the help of higher-level feedback mechanisms.

Although we have still limited knowledge on the neural processes behind chromatic motion, previous psychophysical literature shows evidence for the interaction of motion and color signals. Nishida, Watanabe, Kuriki, and Tokimoto (2007) reported a unique effect of motion on color perception called motion-induced color mixing. They showed that color signals are integrated not only at the same location but also along the motion trajectory by the visual system. Their findings suggested that the visual system integrates color information along the motion trajectory to increase the signal-to-noise ratio for the dynamic object and decrease the motion blur and detect the veridical colors of moving objects. Additionally, Hisakata, Nishida, and Johnston (2014) investigated the phase-dependent contrast sensitivity, demonstrated by Roach et al. (2011), using isoluminant red-green gratings. They reported a lack of phase-dependent contrast sensitivity modulation with isoluminant gratings. However, they reported a motion masking effect where the inducer grating decreased the sensitivity for the isoluminant target grating.

In Chapter 3 experiment 1, I will use a similar stimulus paradigm with Hisakata et al. (2014) to investigate the phase-dependent contrast sensitivity with isoluminant gratings. I will also use luminance-defined chromatic gratings to investigate the interaction of luminance and chromatic signals in this phase-dependent contrast sensitivity modulation. Additionally, in Experiments 3A and 3B, I will look at the effect of smooth pursuit eye movements in this phase-dependent contrast sensitivity modulation using a similar stimulus configuration.

1.5 Smooth pursuit eye movements and contrast sensitivity

Smooth pursuit eye movements are steady, continuous movements of the eyes that make up for the target's motion (Krauzlis, 2005). Although they help to keep the target object at the fovea, eye movements exert challenges for the visual system. In order to perceive a stable world during smooth pursuit eye movements, the retinal motion caused by the eye movements must be separated from the retinal motion caused by object motion. The visual system achieves this task by integrating the efference copy of the motor command and the retinal motion signals (von Holst, & Mittelstaedt, 1971).

The latency of human smooth pursuit eye movements to a moving visual object is about 80–120 ms (Krauzlis, 2004). Pursuit eye movements consist of two different phases, open and close loops. Approximately the first 140 ms of the eye movement is called the open-loop phase. During this phase, the pursuit is mainly guided by the retinal image velocity of the object. The eye accelerates in the target's direction at first, then slows down to match the target's speed. A negative feedback loop appears to decrease the velocity error of the eyes during the closed-loop phase (Spering & Montagnini, 2011). In the primate brain, area MT is responsible for the initiation of the smooth pursuit (Keller & Heinen, 1991), while both MT and MST were found to be responsible for the maintenance of the smooth pursuit eye movements (Their & Ilg, 2005).

Although the effects of saccadic eye movements on perception are known to be destructive in general (Burr, Morrone, & Ross, 1994; Khurana & Kowler, 1987; Ross, Morrone, & Burr, 1997), smooth pursuit eye movements have a more complex interaction with the visual system, demonstrating both suppressive (Schütz, Braun, &

Gegenfurtner, 2007a; Schütz, Delipetkos, Braun, Kerzel & Gegenfurtner, 2007b) and facilitative effects (Chen, Valsecchi & Gegenfurtner, 2017; Schütz, Braun, Kernel, & Gegenfurtner, 2008).

An attenuation effect of contrast sensitivity for achromatic stimulus during the smooth pursuit eye movements was explained by cath-up saccades during the onset of pursuit initiation (Schütz et al. 2007a) and attentional processes involved in both saccadic (Schütz et al. 2007a) and pursuit eye movements (Schütz et al., 2007b). In contrast, for luminance-defined stimuli of high spatial frequency, contrast thresholds were shown to improve during smooth pursuit eye movements. This improvement was explained by a boost in the parvocellular system caused by smooth pursuit eye movements (Schütz et al., 2008).

In support of a boost in the parvocellular system theory caused by eye movements, Schütz et al. (2008) showed that contrast sensitivity for chromatic signals was increased during smooth pursuit eye movements. They argued that smooth pursuit eye movements enhance the activity in the parvocellular pathway to increase object recognition and decrease motion blur caused by the extrastriate signals. Furthermore, in a follow-up study Schütz, Braun, and Gegenfurtner (2009), showed that increased sensitivity to colored stimuli during smooth pursuit eye movements is not a result of speeding up the temporal impulse response in the system. Instead, it results from an increased contrast gain at all temporal frequencies, which increases the overall temporal resolution of the system. Additionally, Chen Valsecchi and Gegenfurtner (2017) showed a general boost in the visual system while observing an isoluminant red and green flickering gratings with smooth pursuit eye movements using steady-state visually evoked potentials (SSVEPs) extracted by

EEG signals from human participants. These enhancements of SSVEPs did not exist when the stimulus was defined by luminance instead of hue changes.

In Chapter 3, Experiments 2, 3A, and 3B will investigate how smooth pursuit eye movements will affect the contrast sensitivity to isoluminant and luminance-defined chromatic gratings.

1.6 Smooth pursuit eye movements and motion perception

Besides sharing similar neuronal substrates in MT and MST, motion perception and smooth pursuit eye movements reveal similar characteristics (Spering, Montagnini, 2011). Additionally, smooth pursuit eye movements can impair and enhance the motion perception for different stimuli. For example, in the Aubert–Fleischl illusion, an object is perceived to be moving slower when it is tracked with smooth pursuit than when observed with stationary eyes (Turano & Heidenreich, 1999). On the other hand, Braun et al. (2008) showed that smooth pursuit eye movements could also enhance the speed judgments when the stimuli are modulated along the color axis.

In addition to these general effects of smooth pursuit eye movements, Terao, Murakami, and Nishida (2015) and Schütz et al. (2007b) reported a direction-specific improvement of smooth pursuit eye movements on motion perception. Schütz et al. (2007b) showed that when the Gabor stimuli moved in the opposite direction of the smooth pursuit eye movement, the visibility of the Gabor decreased compared to the Gabor targets moving in the same direction as the pursuit. They argued that feature-based attention plays a role in this directional selectivity where the visual system prefers the drift direction that is congruent with the eye movements. On the other hand, Terao et al. (2015) reported that a counterphase grating, consisting of two gratings moving in opposite directions (ambiguous motion direction), is perceived to be moving in the opposite direction of the eye movements during the pursuit. They argued that smooth pursuit eye movements enhance the motion of the grating moving opposite to eye movement direction. This finding contradicts Schütz et al. (2007b), where the visibility of a Gabor stimulus moving in the same direction as the eye movements is higher compared to a Gabor stimulus moving in the opposite direction. Terao et al. (2015) suggested that the reason why the two studies found different results is because they were conducted using different contrast levels. Schütz et al.(2007b) used threshold level contrasts to measure detection thresholds. Terao et al.(2015) , on the other hand, used suprathreshold to measure the perceived motion direction. Therefore, they concluded that an object's luminance properties could modulate the effect of smooth pursuit eye movements on the perception of motion direction.

In addition to the contrast sensitivity and motion direction detection tasks, Tong, Ramamurthy, Patel, Vu-Yu, and Bedell (2009) measured the temporal impulse response function (TIRF) during smooth pursuit eye movements. They found that the visual processing speed increased during smooth pursuit eye movements compared to the conditions, where the eyes were fixated. This increase was higher when the grating motion was in the opposite direction of the eye movements. Tong et al. (2009) suggested that speeding up the temporal system reduces the motion smear during smooth pursuit eye movements. It is known that speeding up the TIRF causes a reduced contrast gain in the magnocellular neurons and reduces the sensitivity for luminance signals (Burr & Morrone, 1996).

It has also been shown that pursuit-induced background motion enhances the temporal fusion frequency of color processing. (Terao, Watanabe Yage, & Nishda, 2010). According to Nishida et al. (2007), signal integration for chromatic signals occurs along the motion trajectory to reduce the motion blur. Terao et al. (2010) argued that extra-retinal signals about pursuit boost the color segmentation for the pursuit induced background motion by enhancing the motion signals in the background motion to decrease the motion blur. The enhancement of the temporal fusion frequency does not occur with both flickering stimuli and stimuli moving in the same direction. From these results, Terao et al. (2010) argued that the enhancement of the temporal fusion frequency of the color signals was not due to a general boost in the parvocellular system as suggested by Schütz et al. (2008), arguing a boost should have enhanced the temporal frequency for flickering stimuli and stimuli moving in the same direction with the eyes.

As seen from the literature, the directional selectivity for motion during pursuit depends on several factors. In Chapter 3, Experiments 2, 3A, and 3B, we will investigate the interaction between chromatic motion and smooth pursuit eye movements on contrast sensitivity by examining the directional selectivity of the smooth pursuit eye movements to the drifting isoluminant and luminance-defined chromatic stimulus.

1.7 Motivation and novelty of the thesis

Previous studies investigated the contextual effects of motion on contrast sensitivity using achromatic abutting gratings while the eyes were fixed (Arnold et al., 2007; Arnold et al., 2014; Roach et al., 2011). Additionally, there is extensive research on the effects of smooth pursuit eye movements on luminance and chromatic contrast sensitivity (Schütz et al. 2007a; Schütz et al., 2007b; Schütz et al. 2008). As a novelty, (1) this thesis investigates the contextual effects of chromatic motion with abutting gratings to understand the role of the parvocellular pathway on the aforementioned phase modulation for the first time in the literature (Experiment 1). It differentiates the role of chromatic and luminance signals for phase modulation. (2) Secondly, it investigates the effects of motion direction on the visibility of chromatic target gratings during smooth pursuit eye movements to better understand the interaction between chromatic motion and smooth pursuit eye movements on chromatic contrast sensitivity (Experiment 2). It reveals different directional selective mechanisms for isoluminant and luminance-defined chromatic motion during smooth pursuit eye movements. (3) Finally, it investigates the contextual effects of chromatic motion with abutting gratings during smooth pursuit eye movements to better understand the effects of smooth pursuit eye movements on the chromatic contrast sensitivity for complex stimuli. It reveals an interaction between smooth pursuit eye movements and drift direction using abutting target and inducer isoluminant gratings.

CHAPTER 2

GENERAL METHODOLOGY

2.1 Participants

Seven observers participated in experiments 1, 2, and 3A. Five of these seven observers also participated in experiment 3B. Participation was voluntary without any compensation or an award. All observers had normal or corrected-to-normal vision. None of the observers reported having color blindness. Three of the participants were researchers involved in this study. The rest of the participants were naïve graduate and undergraduate students at Boğaziçi University. The study was compliant with the university research ethics requirements and approved by the Boğaziçi University Ethics Coordinating Committee. Confidentiality and anonymity were ensured by saving data using the subject ID’s. Since all participants were native Turkish speakers, the consent form and the experimental instructions were given in Turkish.

2.2 Stimuli and apparatus

In all experiments, stimuli were presented on a CRT Monitor (Philips 109B40/20) with a refresh rate of 75 Hz and pixel resolution of 1280x1024) driven by Cambridge Research Systems Bits # with 14-bit resolution. MATLAB software was used on HP ProDesk 400 G3 Bussines PC with Windows 8 operating system to execute the experiments. The visual stimuli were manipulated using functions coded on PsychToolbox MATLAB (Brainard & Vision, 1997).

Spyder 4 Elite was used to measure the spectra of the red, green, and blue phosphors at their maximum intensity. The primaries of the monitor had x, y, Y (CIE) coordinates of 0.64, 0.34, 22.64 (red); 0.33, 0.59, 68.14 (green); and 0.17, 0.10, 10.86 (blue). The measured luminance of the screen was 65.6 cd/m². Eye position signals were recorded with a desk-mounted eye tracker (Tobii X1 Light Eye Tracker, Tobii Technology, Stockholm, Sweden) with a sampling rate of 30 Hz. The display was viewed binocularly from a distance of 57 cm. The head position was maintained using a chin rest.

For Experiment 2, a low contrast target grating (width and height = 1°, spatial frequency = 1 c/°) was presented below or above the fixation point. For Experiments 1, 3A, and 3B, two different gratings were used. In addition to the target grating, two high contrast inducer gratings (width = 6.67°, height = 1°, spatial frequency = 1 c/°) were displayed below and above the fixation point, where one of them abutted the target grating horizontally. In Experiment 1, the envelope of the gratings and the eyes were stationary. For Experiments 2, 3A, and 3B, the envelopes and the eyes moved at a 9 deg/sec speed. The sinusoidal waveform of the gratings moved with a drift rate of 4 deg/sec in all experiments. A gaussian blur filter was applied to the width of the inducer with a standard deviation of 0.23° in each direction to reduce the edge detection. The stimuli were presented on a gray background. For the experiments where the inducer grating was present on the screen (experiments 1, 3A, and 3B), the waveform of the target was either in-phase with the inducer gratings' waveform (0°) or advanced by half of a cycle (180°) as it can be seen it the Figure 1.

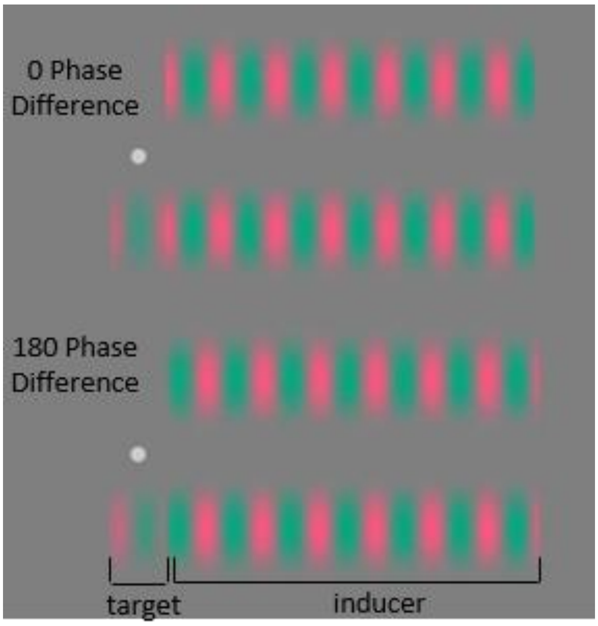


Figure 1. Stimulus configuration for the phase difference between the target and inducer gratings

When the target and inducer were in phase (0-degree phase difference), the target seems like a low contrast extension of the inducer. When the target and inducer were out of phase (180-degree phase difference), the sinewave of the target was advanced by half of a cycle.

Visual stimuli in the experiments were sinusoidal sinewave gratings. The gratings consisted of sinusoidal modulations of chromaticity, or both luminance and chromaticity. The isoluminant gratings were modulated around the white point between magenta and cyan to isolate the L–M color-opponent mechanism (Derrington & Krauskopf, 1984). Individual isoluminance points were determined for each observer using the minimum motion technique (Anstis, Cavanagh, 1983). Individual isoluminance settings were created using these values by combining chromatic gratings with low contrast achromatic gratings, resulting in subtle modulations of the violet–yellow opponent mechanism. For luminance-defined chromatic gratings, 50 % and 100 % Michelson contrast modulations were added to the violet–yellow opponent mechanism. Figure 2 shows the different luminance profiles used throughout the experiment.

Figure 2. An example of different luminance profiles used throughout the experiments.

The first stimulus configuration represents the physical isoluminant stimuli. The second one represents the luminance-defined chromatic grating with 50 % luminance contrast modulation, and the third one represents the luminance-defined chromatic grating with 100 % luminance contrast modulation.

2.3 Procedure

Participants signed the consent form and filled out a demographic form before the experiments. At the beginning of each block, participants received verbal instructions. The same setup was used throughout the experiments in a dark, quiet cubicle at VisionLab, Boğaziçi University. Participants were seated in a chair where their head was placed on a chinrest 57 cm away from the computer screen. Therefore, parameters such as speed and size were standardized, and artifacts were eliminated due to head movements.

All experiments were designed according to psychophysical methodologies. Before the experimental blocks, the isoluminance point for each participant was assessed using the minimum motion technique (Antis & Cavanagh, 1983). After instructions and isoluminant point assessment, participants performed a calibration for eye movement recordings at the beginning of each block. Following the calibration, participants received 7 training trials introducing the stimuli and the task of the block. Blocks consisted of either 140 or 280 trials and lasted around 15 to 20 minutes. In Experiment 1, blocks were separated according to the independent variable of the phase difference between the target and the inducer. Experiment 2 was consisted of 2 blocks for the designated type of stimuli, where one block included eye movements, and the other block was conducted during steady fixation. For every variant of Experiment 3, blocks were separated according to the independent variables of the phase difference between the target and the inducer and the target’s position on the eye movement trajectory.

Participants reported whether the low contrast target stimulus appeared below or above the screen in a 2-AFC task for all the experiments by pressing up and down arrow keys. The contrast level of the low contrast target stimulus was manipulated according to the method of constant stimuli and varied between 6 equally log-spaced values. Each contrast value was presented 20 times in a random order. In addition to the low contrast values, the contrast value of 0 (invisible stimulus) was also presented and shuffled across trials. Although presented during the experimental blocks, the responses from the contrast value of 0 (no signal) were fixed at a percent correct value of %50 during the data analysis to get a more precise psychometric function. The 6 contrast values of the method of constant stimuli differed for isoluminant and luminance-defined chromatic stimuli since the detection of isoluminant stimuli was harder than luminance-defined chromatic stimuli. For each experiment, participants first finished the blocks containing isoluminant stimuli in a random order then move onto the blocks with luminance-defined chromatic stimuli in the order of 50% and 100% where it is related.

2.4 Data analysis

Responses for each trial were collected during the experiment and saved in a MATLAB data file after each block. Individual psychometric functions were fitted with a cumulative gaussian function and detection thresholds were calculated at the 75% correct performance using the psignifit toolbox version 2.5.6 for MATLAB, which implements the maximum-likelihood method described by Wichmann and Hill (2001). Log-contrast thresholds were determined and saved in an excel file for each condition and each participant.

For Experiment 1, three two-by-two within-subject ANOVA were conducted with the independent variables of phase difference and target's position relative to the drift direction for all types of stimuli. For Experiment 2, three three-way ANOVA were conducted for each of the three different stimuli types. For Experiment 3A, two 2x2x2 ANOVA were conducted with the independent variables of phase difference, target's position relative to drift direction, and target's position relative to eye movement trajectory. For Experiment 3B, four paired samples t-tests (together with Boferroni corrections) were conducted between the two conditions with each inducer size and stimulus type. Data were analyzed using SPSS.

2.5 Eye movement analysis

We obtained eye velocity signals by digitally differentiating the eye location signals over time. The eye velocity was divided by the pursuit target velocity to calculate the pursuit gain. The pursuit gain using the eye velocity signals was computed from a time point that corresponded to 300 ms after the motion of the target began on the screen. Those trials with the pursuit gain higher than 1.5 were eliminated from the data analysis. We did not implement any filter to smooth the signals for the eye position or the eye velocity. To compensate for the internal noise of the eye tracker caused by the lack of smoothing and a long pursuit time interval, we choose a high cut-off point for the pursuit gain. To detect saccades, we used a cut-off criterion (95,000 deg/s3) on the third derivative of eye position (Wyatt, 1998). The data of the trial was removed from the analaysis if a saccade was detected 300 ms after the stimulus started to move on the screen. The intervals were considered as smooth pursuit eye movement if the position shift of the eye gaze position on the x-axis remained between +/- 3 degrees for at least 700 ms from the moment the stimulus started to move towards 1400 ms afterwards. Those trials which failed to meet these criteria were omitted. Only 2 out of 7 participants met all of these criteria. Although the valid number of trials in some of the experimental blocks of the excluded participants was sufficient, these participants were not included in the further analyses as enough trials could not be achieved in all conditions. Three of the participants wore glasses or contact lenses. We believe that the glasses or contact lenses caused calibration problems in the eye tracking procedure. In addition to the eliminated trials due to the criteria described above, there were also trials in which the eye-tracking device did not follow any eye gaze or recorded only a small number of eye gaze data ($n < 4$). The trend in the effects of the 2 participants, whose data were double-check by both keeping the full data or eliminating the trials which did not meet the eye movement analyses criteria, however, coincided in terms of the main trends. Thus, we ran our statistical analyses without the removal of any trials and keeping all subjects' data.

CHAPTER 3

EXPERIMENTS

3.1 Experiment 1

Motion inside of an achromatic static grating can modulate the visibility of a low contrast target, abutting the high contrast inducer (Arnold et al., 2007; Roach et al., 2011; Arnold et al., 2014). Arnold et al. (2007) found that the target in the leading edge is more visible than the target in the trailing edge. Roach et al. (2011) discovered that this effect is phase-dependent on the leading edge, where the visibility only increases when the target and inducer phases are congruent with each other. They suggested a forward prediction model where a summation between targets' sensory input and an internal prediction increases the target's visibility leading the motion. However, Arnold et al. showed that the phase dependency also occurs at the trailing edge, although in a smaller magnitude. They suggested a spatial summation mechanism at both edges where motion deblur mechanisms decrease the spatial summation in the trailing edge.

In Experiment 1, we investigated this mechanism using isoluminant and luminance-defined chromatic stimuli to understand the role of the parvocellular pathway in motion perception. The purpose of the experiment was to see (1) whether phase modulation at the trailing and leading edges occur for the isoluminant and luminance-defined chromatic gratings, (2) whether the visibility of the target in the leading edge would be higher compared to the visibility in the trailing edge and (3) whether different mechanisms play a role for isoluminant motion perception compared to luminance-defined chromatic motion perception.

3.1.1 Participants

Seven observers participated in the experiment. Three of the participants were researchers involved in this study. The rest of the participants were naïve graduate and undergraduate students at Boğaziçi University. All participants participated in the experiments voluntarily and had normal or corrected to normal vision. None of the participants reported to have color blindness.

3.1.2 Stimulus

The stimulus for this experiment was isoluminant and luminance-defined chromatic sinusoidal sinewave gratings. The luminance-defined chromatic sinusoidal gratings were modulated by either 50% or 100% luminance difference between magenta and cyan signals. The target grating (width and height = 1°, spatial frequency = 1 c/°) was displayed either 1° below or above the fixation point in the middle of the screen. Two high contrast inducer gratings (width = 6.67°, height = 1°, spatial frequency = 1 c/°) were displayed below and above the fixation point (with a radius of 0.4°) where they could abut the target grating horizontally. Inducers were presented either to the left or right of the target grating randomly. The sinusoidal pattern of both target grating and inducer gratings drifted in the same direction, either to the left or right, with a speed of 4 deg/sec. As shown in Figure 3, the leading and trailing positions of the target were determined by the direction of drift according to the inducer motion (drifting towards or away from the target). The target waveform was either in-phase (0° shift) or out of phase (180° shift) with the inducer.

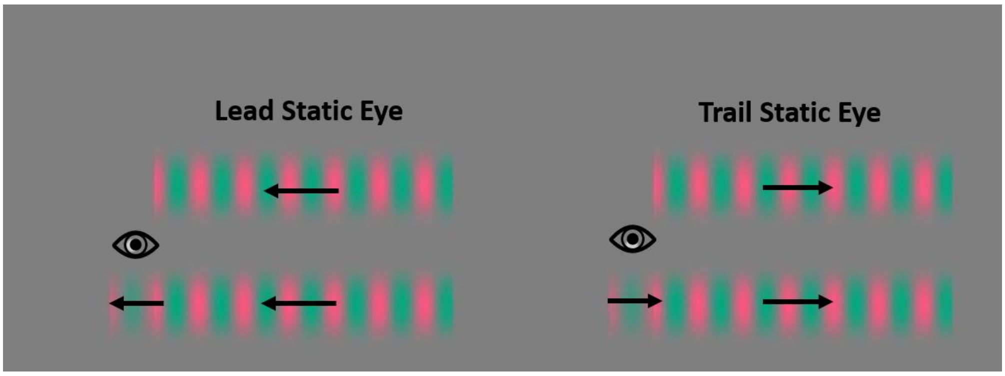


Figure 3. Target position conditions for Experiment 1.

According to the drift direction of the gratings, the target could be in the leading or training position. If the drift direction is towards the target, the target is leading the inducer. If the drift direction is away from the target, the target is trailing the inducer.

3.1.3 Procedure

After the calibration for the eye tracker in each block, participants initiated the experiment by pressing a key on a keyboard. After the keypress, the fixation point appeared in the middle of the screen for 500ms. Participants were instructed to fixate their eyes on the fixation point throughout the experiment. After 500ms, drifting sinusoidal gratings appeared and remained on the screen for 2.6 seconds. Participants were asked to report whether the target grating appeared above or below the fixation point by pressing the up and down keys. Figure 4 shows the experimental procedure.

While leading and trailing conditions were presented in the same block randomly, in-phase and out-of-phase conditions were presented in different blocks. Additionally, participants completed a baseline condition where the target grating appeared on the screen without inducer gratings in a separate block (which was the steady fixation condition of Experiment 2). The blocks where inducer gratings were present were consisted of 280 trials. The baseline condition consisted of 140 trials. Each block took around 15 to 20 minutes to complete. Each participant performed different blocks in a random order. Participants first completed the blocks containing the isoluminant stimuli and moved on to complete the blocks containing luminance-defined chromatic stimuli with 50% and 100% luminance contrasts.

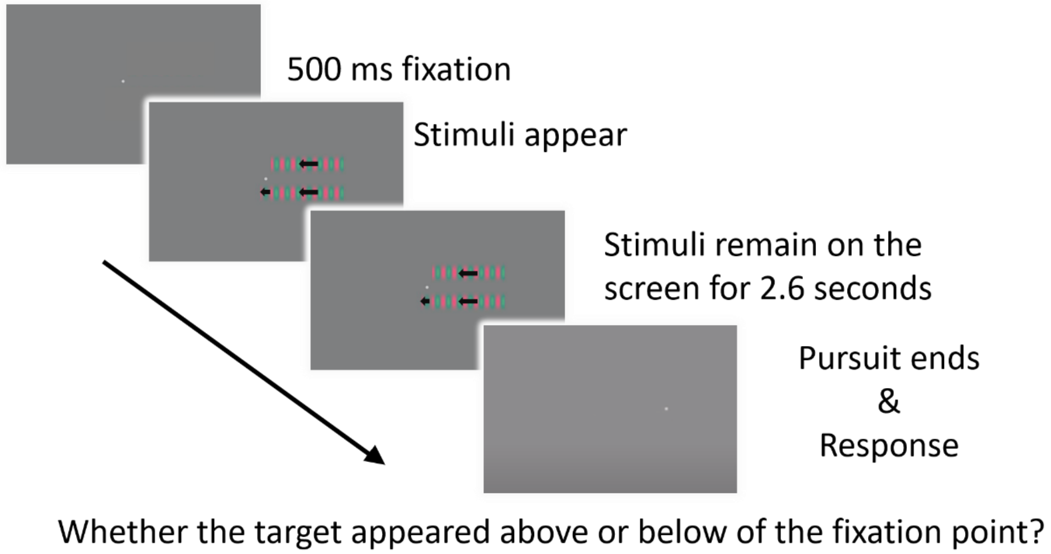


Figure 4. Outline of Experiment 1.

At the beginning of each trial, the fixation point appeared on the screen’s right or left side. After 500 milliseconds, the stimulus configuration for the block appeared on the screen for 2.6 seconds with the fixation point. Participants fixated on the fixation point for this whole time. After 2.6 seconds, the stimulus disappeared, and participants reported their responses by pressing up or down arrow keys on the keyboard.

3.1.4 Results

A two-by-two repeated measures ANOVA was conducted with target position (leading and trailing) and phase difference (0° and 180°) as within-subject factors.

For the isoluminant stimuli the results of the two-way repeated-measures ANOVA revealed that there was no main effect of either phase difference ($F(1,6) = .99$, $p = .33$, $\eta_p^2 = .16$) or target position ($F(1,6) = 1.12$, $p = .12$, $\eta_p^2 = .36$). Log contrast threshold was similar when the phase difference between the inducer and the target was 0° (*M* = .44, *SEM* = .06) and 180° (*M* = .47, *SEM* = .05) or when the target was in the leading position (*M* = .43, *SEM* = .05) and trailing position (*M* = .47, *SEM*

= .05). Similarly there were no interactions between phase and target position (*F*(1,6) = 2.61, *p* = .16, η_p^2 = .30). The phase difference between the target and inducer did not change the visibility of the target neither in the leading position (*F*(1,6) = .02, *p* = .89, η_p^2 = .004) nor in the trailing position (*F*(1,6) = 2.15, *p* = .20, η_p^2 = .26) significantly. However, as it can be seen in the Figure 5, there was a phase modulation for the target on the trailing edge as a trend. Moreover, the target's visibility with 0° phase difference was also increased in the presence of the inducer pattern with respect to the baseline condition as a trend.

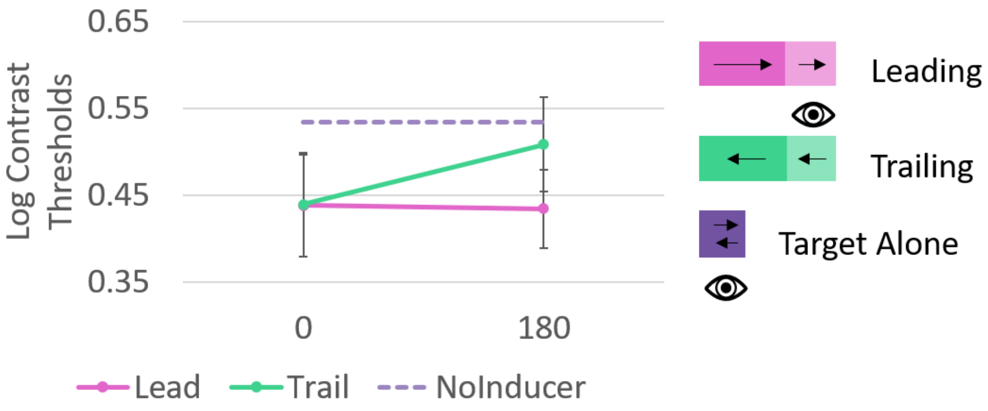


Figure 5. Overall results for isoluminant stimuli in Experiment 1, where eyes were steady on a fixation point.

Log contrast thresholds are represented in the y-axis. On the x-axis, two levels of the phase difference condition (0° and 180°) are shown. While the green line represents the trailing position, the pink line represents the leading position. The purple line represents the baseline condition where no inducer was abutting the target. Error bars indicate the standard errors of the mean (+/- 1 *SEM*).

For the luminance-defined chromatic stimuli with 50% luminance contrast between magenta and cyan signals, the results of the two-way repeated-measures ANOVA revealed that there was a main effect of target position (*F*(1,6) = 6.04, *p* = .05, η_p^2 = .50) and phase difference (*F*(1,6) = 9.29, *p* = .02, η_p^2 = .61). Log contrast threshold was smaller when target was in the trailing position (*M* = .07, *SEM* = .07) than when it was in the leading position ($M = .15$, $SEM = .07$) and when the phase difference between the target and inducer was 0° ($M = .05$, $SEM = .09$) than when it was 180° ($M = .17$, $SEM = .06$). Additionally, there was an interaction between the phase difference and target position ($F(1,6) = 9.52$, $p = .03$, $\eta_p^2 = .62$). When target was in the trailing position, log contrast thresholds in 0° phase difference ($M = -.02$, $SEM = .10$) were smaller than those in 180° phase difference condition ($M = .16$, $SEM = .06$) ($F(1,6) = 11.47$, $p = .02$, $\eta_p^2 = .66$). This difference between 0° ($M = .12$, $SEM = .08$) and 180° ($M = .18$, $SE = .06$) phase differences disappeared when the target was in the leading position ($F(1,6) = 3.26$, $p = .12$, $\eta_p^2 = .35$). Figure 6 shows this interaction.

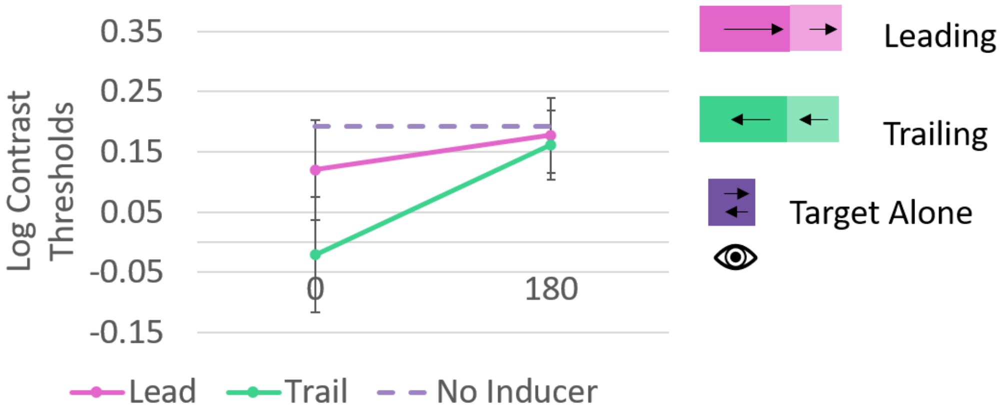


Figure 6. Overall results for the luminance-defined chromatic stimuli with 50% luminance contrast in Experiment 1, where eyes were steady on a fixation point.

Log contrast thresholds are represented in the y-axis. On the x-axis, two levels of the phase difference condition (0° and 180°) are shown. While the green line represents the trailing position, the pink line represents the leading position. The purple line represents the baseline condition where no inducer was abutting the target. Error bars indicate the standard errors of the mean (+/- 1 *SEM*).

For the luminance-defined chromatic stimuli with 100% luminance contrast between magenta and cyan phases, the results of the two-way repeated-measures ANOVA revealed that there was a main effect of phase difference ($F(1,6) = 6.14$, $p <$

$.05$, $\eta_p^2 = .51$). Log contrast threshold was smaller when the phase difference between the target and inducer was 0° ($M = -.30$, $SEM = .07$) than when it was 180° ($M = -.15$, $SEM = .07$). There was no significant difference between the log contrast threshold when the target was in the leading and trailing position ($p > .05$). Although there was no interaction between phase and target position ($p > .05$), there was a phase modulation in the leading edge. When target was in the leading position log contrast thresholds for 0° phase difference ($M = -.30$, $SEM = .07$) was smaller than 180° phase difference ($M = -.10$, $SEM = .01$) ($F(1,6) = 8.35$, $p = .03$, $\eta_p^2 = .58$). Figure 7 demonstrate the phase modulation at both edges.

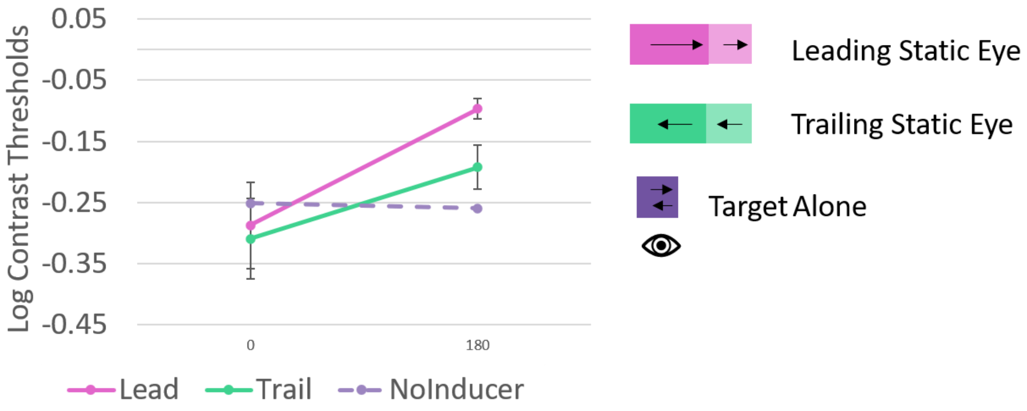


Figure 7. Overall results for the luminance-defined chromatic stimuli with 100% luminance contrast in Experiment 1, where eyes were steady on a fixation point.

Log contrast thresholds are represented in the y-axis. On the x-axis, two levels of the phase difference condition (0° and 180°) are shown. While the green line represents the trailing position, the pink line represents the leading position. The purple line represents the baseline condition where no inducer was abutting the target. Error bars indicate the standard errors of the mean (+/- 1 *SEM*).

3.1.5 Summary and Discussion

Experiment 1 revealed that for isoluminant stimuli, although it was not significant, there was a phase modulation at the trailing edge of the inducer. The trend was that the presence of the inducer grating facilitated the target’s visibility at the trailing edge for the in-phase (0° phase difference) condition. The phase modulation at the trailing edge became even more prominent (and significant) when a 50% luminance difference was added to the magenta and cyan signals. In this condition, the target's visibility was also significantly higher at the trailing edge compared to the leading edge. Thus, for isoluminant stimuli, it seems that the presence of the inducer grating facilitates the visibility of the target at the trailing edge. Interestingly, on the other hand, when the luminance contrast was increased to 100%, the phase modulation at the trailing edge became non-significant, although still remained as a trend. In this condition, it is rather the phase modulation at the leading edge which became significant, an effect which was not existent in the isoluminant and %50 luminance contrast conditions.

In sum, we observed a phase modulation at the trailing edge for the isoluminant and luminance-defined chromatic gratings with 50% luminance contrast. However, for both stimuli, there was no phase-dependent sensitivity modulation at the leading edge. The lack of phase modulation at the leading edge can be explained by the motion-induced color-mixing effect, where integration of chromatic signals along the motion trajectory occurs only at the leading edge (Nishida et al., 2007). This integration of the color signals may make the phase dependency for the motion-induced contrast sensitivity redundant at the leading edge since the cyan and magenta signals get integrated to result in a percept of gray. However, as luminance signals are added to the stimuli, the phase modulation at the leading-edge increases, which aligns well with the previous literature showing the phase modulation at the leading edge using achromatic stimuli (Arnold et al.,2014; Roach et al., 2011). These results demonstrate that the phase modulations at the leading and trailing edges depend on different neural mechanisms.

Another interesting result was the improved visibility of the target at the trailing edge compared to the target at the leading edge for luminance-defined (%50 contrast) chromatic stimuli. Previous literature using achromatic stimuli has consistently reported higher sensitivity for the target at the leading edge of the inducer (Arnold et al., 2007; Arnold et al., 2014; Roach et al., 2011). Therefore, our current result is in contradiction with the previous literature. This facilitation effect could not be explained by the flank facilitation, since there would have to be a gap between the target and flankers for facilitation to occur in contrast sensitivity (Polat & Sagi, 1993). Although we can eliminate several possible mechanisms which can lead to a facilitation of the target at the trailing edge, our results are not able to suggest a possible mechanism to explain this result. Therefore, the mechanism responsible for this facilitation is still in question.

Our findings demonstrate an interaction between color and luminance signals for the motion-induced phase-dependent contrast sensitivity. Using fMRI, Mullen, Chang and Hess (2015) demonstrated that most of the interaction between chromatic and luminance signals occurs at the early cortical areas such as area V1 and V2. However, most of the literature suggests that the chromatic motion perception occurs rather at the extrastriate cortex such as a pathway between the area V3 an V4 (Gegenfutner & Hawken, 1996) or area MT (Cropper & Wuerger, 2005). Here, we suggest that feedback mechanisms from area V3, V4 or MT to the area V1 and V2 might be responsible for the motion-induced contrast sensitivity changes we observed in this experiment.

3.2 Experiment 2

Schütz et al. (2008) showed that the sensitivity to an isoluminant line stimulus is increased during smooth pursuit eye movement. Additionally, Schütz et al. (2007b) and Terao et al. (2015) demonstrated that the internal drift direction of a sinewave envelope could modulate its visibility during smooth pursuit eye movements.

Experiment 2 aimed to investigate the visibility of isoluminant and luminance-defined chromatic target stimuli during smooth pursuit eye movements. We first aimed to investigate whether the sensitivity increase reported by Schütz et al. (2008) during smooth pursuit eye movements can be replicated using isoluminant and luminance-defined chromatic drifting target gratings. Our second purpose was to investigate the directional selectivity for motion on chromatic contrast sensitivity during smooth pursuit eye using isoluminant and luminance-defined chromatic gratings.

3.2.1 Participants

All 7 observers participated in the experiment. Three of the participants were researchers involved in this study. The rest of the participants were naïve graduate and undergraduate students at Boğaziçi University. All participants participated in the experiments voluntarily and had normal or corrected to normal vision with normal color perception.

3.2.2 Stimulus

The stimuli for this experiment were isoluminant and luminance-defined sinusoidal sinewave target gratings (width and height = 1°, spatial frequency = 1 c/°), which were displayed either 1° below or above the fixation point in the middle of the screen. As in Experiment 1, the luminance-defined chromatic sinusoidal gratings were modulated by either 50% or 100% luminance difference between magenta and cyan signals. In Experiment 2, the target grating was presented alone without the presence of inducers. The target and fixation point either appeared in the middle of the screen and remained fixated or appeared on the right or left side of the screen and moved horizontally with a 9 deg/sec speed rate. The sinewave of the grating drifted with a rate of 4 deg/sec either in the same or opposite direction of the pursuit (to the right or left in the fixation condition). The drift directions can be seen in Figure 8.

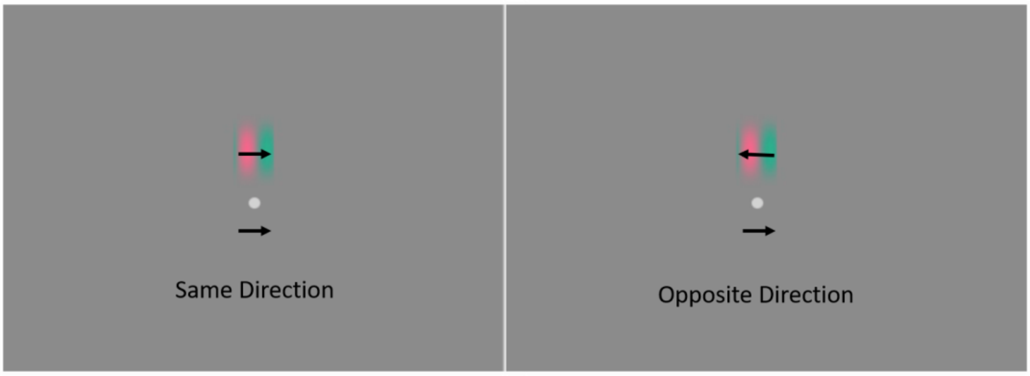


Figure 8. Stimulus configuration for Experiment 2.

The target's drift direction could either be in the same or opposite direction as the eye movement.

3.2.3 Procedure

After the calibration for the eye tracker in each block, participants initiated the experiment by pressing a key on the keyboard. After the keypress, the fixation appeared on the screen for 500ms. Participants were instructed to fixate their eyes on the fixation point throughout the experiment. After 500ms, the drifting sinusoidal target grating appeared on the screen and moved either horizontally (together with the eye movement) or remained fixated (no eye movement) on the screen for 2.6 seconds. Observers reported whether the target grating appeared above or below the fixation point by pressing up and down keys. Figure 9 shows the experimental design.

The experiment consisted of 2 blocks for one stimulus type. In one block, the target and the fixation were moving horizontally on the screen, whereas in the other block, the envelope of the dynamic target and the fixation point remained static in the middle of the screen. While the fixation block was 140 trials, the smooth pursuit block was 280 trials with the same direction drift and opposite direction drift conditions. The blocks took around 15 to 20 minutes to complete. Each participant performed different blocks in random order. Participants first completed the blocks containing isoluminant stimuli and moved on to complete the blocks containing luminance-defined chromatic stimuli with 50% and 100% luminance contrasts.

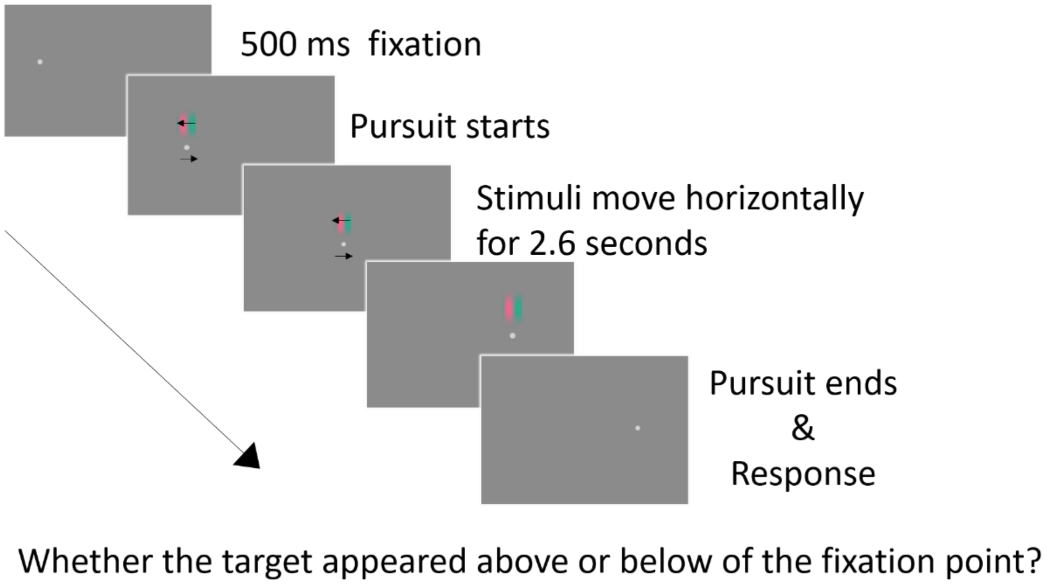


Figure 9. Outline of Experiment 2.

At the beginning of each trial, the fixation point appeared on the screen’s right or left side. After 500 milliseconds, the stimulus configuration for the block appeared on the screen and moved horizontally along the screen for 2.6 seconds with the fixation point. Participants followed the fixation point for this whole time. After 2.6 seconds, the stimulus disappeared, and participants reported their responses by pressing up or down arrow keys on the computer.

3.2.4 Results

For isoluminant stimuli, the data violated the sphericity assumption. Therefore, the results were presented with Greenhouse-Geisser correction. A one-way repeated measures ANOVA results revealed a significant difference between the log contrast thresholds of the target stimuli ($F(1.15,6.79) = 6.78$, $p = .03$, $\eta_p^2 = .53$). Post-hoc comparisons indicated that the difference between log contrast thresholds for the target drifting the opposite way of the eye pursuit ($M = .41$, $SEM = .06$) and target drifting the same way of the eye pursuit ($M = .45$, $SEM = .07$) were not different from each other ($p > .05$). However, as shown in Figure 10, the visibility of the target drifting oppositely to the eye movements was higher than the target drifting in the same direction as the eye movements. There was a significant difference between the dynamic target observed during fixation ($M = .54$, $SEM = .07$) and the dynamic target drifting in the opposite direction of the eye pursuit ($p = .04$). There was also a significant difference between the dynamic target observed during fixation and the target drifting in the same direction as the eye movement ($p = .02$).

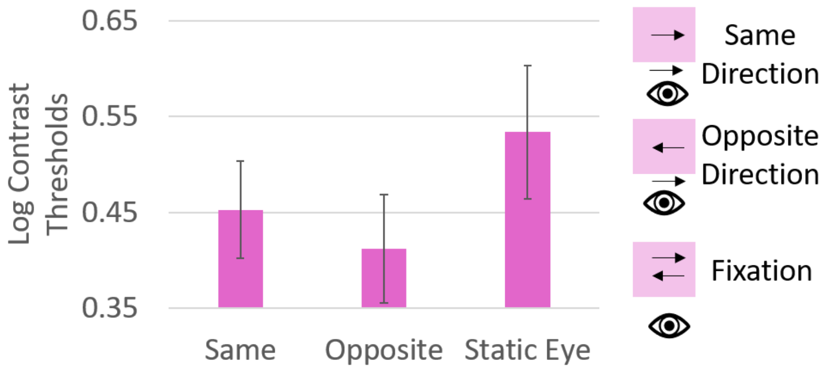


Figure 10. The visibility of the iso-luminant target grating during fixation and smooth pursuit eye movements.

Log contrast thresholds are represented in the y-axis. On the x-axis, three levels of the eye movement condition (Same, opposite, and fixation) are shown. Error bars indicate the standard errors of the mean (+/- 1 *SEM*).

For the luminance-defined chromatic stimuli with 50% luminance contrast between magenta and cyan signals, the results of a one-way Repeated Measures ANOVA revealed that there was a significant difference between the log contrast thresholds of the target stimuli ($F(2,12) = 5.79$, $p = .02$, $\eta_p^2 = .49$). Post-hoc comparisons indicated that the log contrast thresholds for the target drifting in the same direction of the eye pursuit ($M = .004$, $SE = .08$) was smaller than log contrast thresholds for the target observed in the absence of eye movements ($M = .19$, $SEM = .10$) ($p = .04$). There was no difference between the log contrast threshold of the target drifting in the opposite direction of the eye pursuit ($M = .10$, $SE = .07$) and log contrast thresholds for the target observed in the absence of eye movements ($p > .07$). There was also no difference between the contrast threshold of the target drifting in the opposite and the same direction of the eye pursuit ($p = .10$). Figure 11 demonstrates the results.

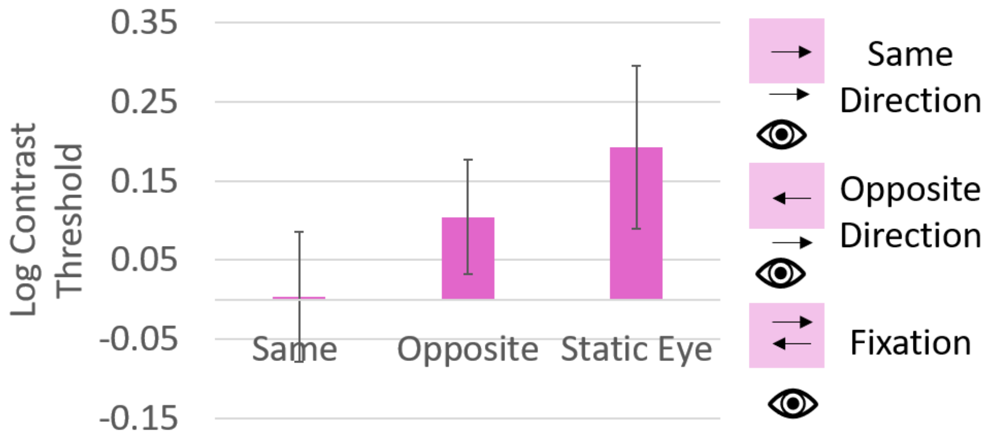


Figure 11. The visibility of the luminance-defined chromatic gratings with 50% luminance contrast during fixation and smooth pursuit eye movements.

Log contrast thresholds are represented in the y-axis. On the x-axis, three levels of the eye movement condition (Same, opposite, and fixation) are shown. Error bars indicate the standard errors of the mean (+/- 1 *SEM*).

For the luminance-defined chromatic stimuli with 100% luminance contrast, a one-way Repeated Measures ANOVA results revealed a significant difference between the log contrast thresholds of the target stimuli ($F(2,12) = 7.76$, $p = .01$, $\eta_p^2 = .56$). Post-hoc comparisons revealed no difference between the log contrast threshold of the target drifting in the opposite direction of the eye pursuit (*M* = -.16, *SEM* = .05) and log contrast thresholds for the target observed in the absence of eye movements (*M* = -.21, *SEM* = .05) ($p > .05$). Similarly, there were no differences between the log contrast threshold of the target drifting in the same direction of the eye pursuit (*M* = -.38, *SEM* = .04) and log contrast thresholds for the target observed in the absence of eye movements (*M* = -.21, *SEM* = .05) ($p > .05$). However, there was a significant difference between the log contrast threshold of the target drifting in the same and the opposite directions ($p = .01$). Figure 12 displays the results.

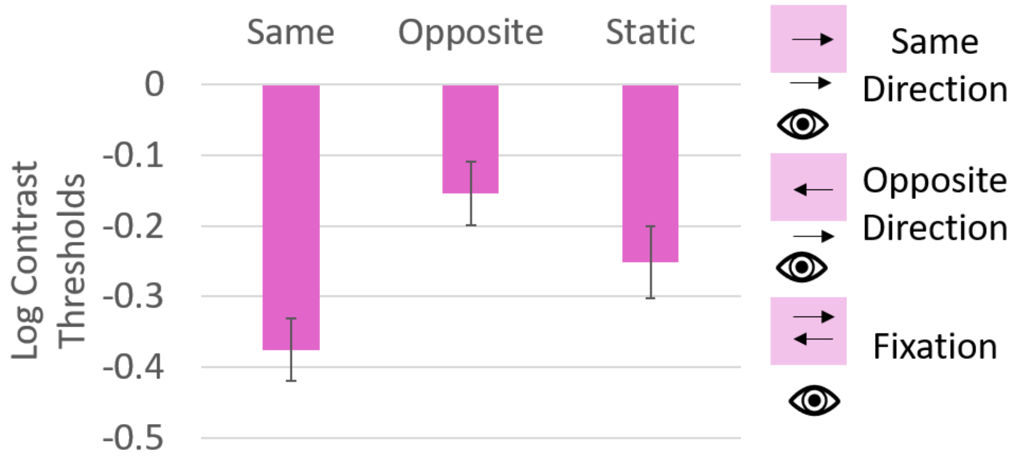


Figure 12. The visibility of the luminance-defined chromatic gratings with 100% luminance contrast during fixation and smooth pursuit eye movements.

Log contrast thresholds are represented in the y-axis. On the x-axis, three levels of the eye movement condition (Same, opposite, and fixation) are shown. Error bars indicate the standard errors of the mean (+/- 1 *SEM*).

3.2.5 Summary and Discussion

Here, we firstly aimed to investigate whether the facilitation of contrast sensitivity to chromatic stimulus during pursuit (Schütz et al., 2008) also occurs for dynamic gratings or not. Our results revealed that for isoluminant and luminance-defined chromatic gratings with 50% luminance contrast, smooth pursuit eye movements facilitated the visibility of the target gratings. However, this facilitation disappeared with luminance-defined chromatic gratings with 100% luminance contrast. Our results are in line with Schütz et al. (2008), where they claimed smooth pursuit eye movements boost the activation of the parvocellular pathway to reduce motion blur and enhance object recognition. Therefore, the visibility of chromatic gratings increases during smooth pursuit compared to fixation. Additionally, our results are in line with Schütz et al. (2007a, 2007b), where for achromatic gratings, smooth pursuit eye movements have a destructive effect on contrast sensitivity. Therefore, with luminance-defined chromatic gratings with 100% luminance contrast, the boost by the parvocellular system gets canceled out by the additional luminance signals. Schütz et al. (2007b) suggested that attentional mechanisms are responsible for attenuating contrast sensitivity for achromatic signals during smooth pursuit eye movements. In their study, observers viewed the target stimulus on their peripheral visual field during the smooth pursuit, which required the allocation of covert attention for its detection. Because pursuit is presumed to have additional cost of attentional mechanisms, Schütz et al. proposed that the performance decreased for the visibility of the eccentric target stimulus during the pursuit. Our stimulus, on the other hand, was presented in the parafovea. Thus, it does not require allocation of covert attention for its detection. We rather suggest that the attenuation of the contrast sensitivity for 100% luminance contrast can be explained by the increase in the TIRF of the visual system during smooth pursuit eye movements (Tong et al., 2009), where speeding up of TIRF reduces the sensitivity to luminance signals (Burr & Morrone, 1996). Currently, we plan to conduct an experiment that measures the TIRF in our current paradigm.

With Experiment 2, our second aim was to investigate the effect of drift direction on contrast sensitivity during smooth pursuit eye movements. Previous literature demonstrated that the drift direction of the target gratings affects their visibility during smooth pursuit eye movements (Schütz et al., 2007b). Here, we showed that the drift direction of the chromatic gratings modulates their visibility, and that this modulation depends on the luminance profile of the target grating. Accordingly, with isoluminant stimuli, the visibility of the gratings drifting in the opposite direction was higher than the gratings drifting in the same direction as a trend. Smooth pursuit eye movements cause objects in the background to move in the opposite direction of the eye movements. This causes motion blur induced by eye movements. Therefore, we hypothesized that if the visual system boosts the activity in the parvocellular system during smooth pursuit (Schütz et al. 2008), boosting the visibility of the target drifting in the opposite direction of the pursuit would increase the signal-to-noise ratio for the objects in the background which in turn would reduce the motion blur caused by the eye movements. On the other hand, this directional selectivity gets reversed for the luminance-defined chromatic gratings. This reversal in the directional selectivity can be explained by the change in the temporal response of the system during smooth pursuit eye movements (Tong et al., 2009). During smooth pursuit eye movements, the TIRF speeds up to reduce motion blur for the objects moving in the opposite direction of the eye movements. It is also known that speeding up the TIRF reduces the sensitivity to luminance signals (Burr & Morrone, 1996). Therefore, the visibility of the luminance-defined chromatic targets drifting in the opposite direction may end up being lower than the targets drifting in the same direction.

3.3 Experiment 3A

Our previous experiments showed that, contextual motion cues from the object and oculomotor cues caused by the eye movements affect the visibility of isoluminant and luminance-defined chromatic objects. Here in Experiment 3A, we examined the interaction between the contextual motion cues and smooth pursuit eye movements on chromatic sensitivity. Therefore, the aim of Experiment 3A was (1) to examine whether the target’s position relative to the eye movement trajectory affects its visibility, (2) whether the relative drift direction of the target and inducer motion affects the target’s visibility during smooth pursuit eye movements, and (3) whether the phase modulation in trailing and leading edges were still prominent during the smooth pursuit eye movements.

3.3.1 Participants

Seven observers participated in the experiment. Three of the participants were researchers involved in this study. The rest of the participants were naïve graduate and undergraduate students at Boğaziçi University. All participants participated in the experiments voluntarily and had normal or corrected to normal vision with normal color perception.

3.3.2 Stimulus

The stimulus for this experiment was isoluminant and luminance-defined chromatic sinusoidal sinewave gratings. The luminance-defined chromatic sinusoidal gratings were modulated by a 50% luminance difference between magenta and cyan signals. The target grating (width and height = 1°, spatial frequency = 1 c/°) was displayed either 1° below or above the fixation point. Two high contrast inducer gratings (width = 6.67°, height = 1°, spatial frequency = 1 c/°) were displayed below and above the fixation point where they could abut the target grating horizontally. Gratings were presented either to the left or right of the target grating. The sinusoidal pattern of both target grating and inducer gratings drifted in the same direction, either to the left or right, with a speed of 4 deg/sec. The target waveform was either in-phase (0° shift) or out of phase (180° shift) with the inducer. Gratings moved on the screen horizontally with a velocity rate of 9 deg/sec.

The placement of the inducer relative to the eye movement trajectory constructed the target's position concerning the eye movement trajectory. If the inducer was in front of the target's movement trajectory, the target was trailing the inducer. If the inducer was behind the target's trajectory, the target was leading the inducer. The drift direction of the inducer and the target determined the target's position relative to the inducer. If the grating pattern was drifting away from the target, the target was in the trailing position. If the grating pattern was drifting towards the target, the target was in the leading position. Therefore, there were four different positions of the target relative to the eye movements and the inducer. The target could lead the inducer through the eye movement trajectory and its drift motion (same direction as the eye movements). It could lead the inducer through the eye movement trajectory and trail it with its drift motion (opposite direction to the eye movements). In opposite, the target could trail the inducer through the eye movement trajectory and lead the inducer with its drift motion (opposite direction). Finally, the target could trail the inducer through the eye movement trajectory and its drift motion (same direction). Figure 13 displays four different conditions for the target positions.

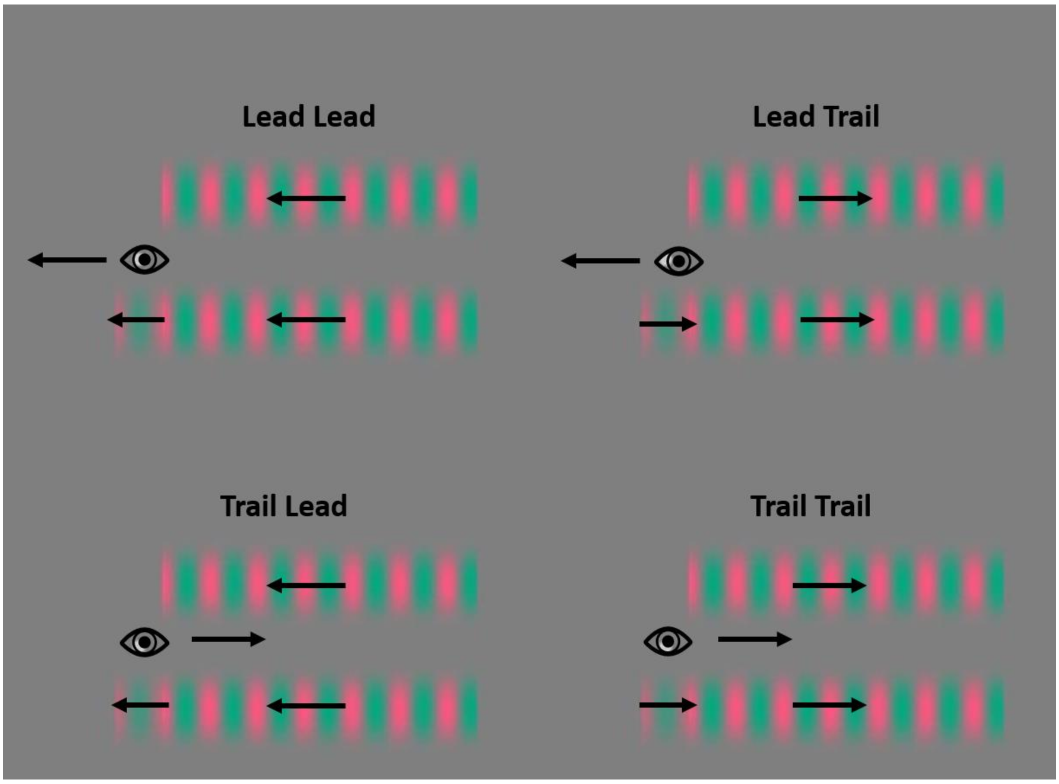


Figure 13. Target position conditions for Experiment 3A.

According to the eye movement trajectory or drift direction of the gratings, the target could be in the leading or training position. The first positions represent the target's position according to the eye movement trajectory. The second positions represent the target's position according to the drift direction.

3.3.3 Procedure

After calibration for the eye tracker in each block, participants started the experiment by pressing a key on the keyboard. After the keypress, the fixation appeared on the screen for 500ms. Participants were instructed to fixate their eyes on the fixation point throughout the experiment. After 500ms, drifting sinusoidal target and inducer gratings appeared on the screen and moved horizontally on the screen for 2.6 seconds. Observers reported the target's position in relation to the fixation point by pressing up and down keys. Figure 14 shows the experimental design.

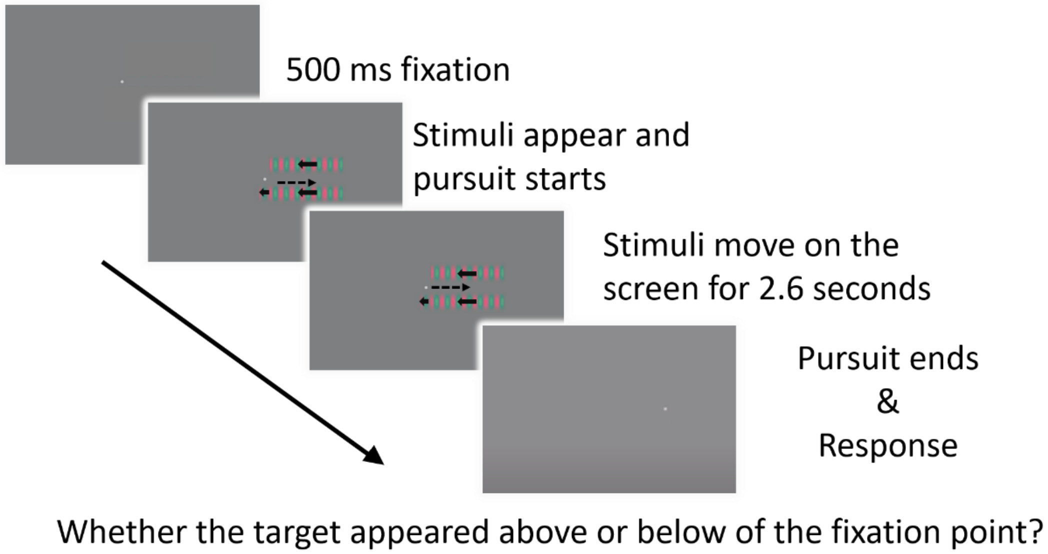


Figure 14. Outline of Experiment 3A.

At the beginning of each trial, the fixation point appeared on the screen's right or left side. After 500 milliseconds, the stimulus configuration for the block appeared on the screen and moved horizontally along the screen for 2.6 seconds with the fixation point. Participants followed the fixation point for this whole time. After 2.6 seconds, the stimulus disappeared, and participants reported their responses by pressing up or down arrow keys on the computer.

While leading and trailing conditions with respect to drift motion were presented in the same block randomly, in-phase, and out of phase conditions were presented in different blocks. Additionally, the target's two different positions according to eye movement trajectory (trail vs. lead) were also presented in different blocks. Therefore, there were 4 different blocks for one stimulus type. Smooth pursuit conditions in Experiment 2 were taken as a baseline for this experiment. The blocks took around 15 to 20 minutes to complete. Each participant performed different blocks in random order. Participants first completed the blocks containing isoluminant stimuli and moved on to complete the blocks containing luminance-defined chromatic stimuli with 50% luminance contrasts.

3.3.4 Results

For the iso-luminant stimuli, the results of a three-way Repeated Measures ANOVA revealed that there was a significant main effect of the target's position with respect to the eye movement trajectory ($F(1,6) = 7.41$, $p = .04$, $\eta_p^2 = .55$). Log contrast thresholds for the target leading the inducer along the eye movement trajectory ($M = .46$, $SEM = .05$) were smaller than the target trailing the inducer along the eye movement trajectory ($M = .48$, $SEM = .04$). Additionally, there was a significant main effect of targets position according to the grating's drift motion ($F(1,6) = 13.36$, $p = .01$, $\eta_p^2 = .69$). Accordingly, log contrast thresholds for the target trailing the inducer, ($M = .45$, $SEM = .05$) were smaller than the target leading the inducer, ($M = .48$, $SEM = .04$). There was no significant phase modulation as a main effect, ($F(1,6) = 2.72$, $p = .16$, $\eta_p^2 = .31$). There was a significant interaction between the inducer position with respect to the eye movement trajectory and the drift motion, ($F(1,6) = 6.17$, $p < .05$, $\eta_p^2 = .51$). Log contrast thresholds for the target in the trailing position with respect to the eye movement trajectory and drift motion (same direction), ($M = .43$, $SEM = .05$) were smaller than the one in the trailing position with respect to the eye movement trajectory but in the leading position with respect to the drift direction (opposite direction), ($M = .52$, $SEM = .04$) ($F(1,6) = 10.55$, $p = .02$, $\eta_p^2 = .64$). There was no difference between the log contrast thresholds for the targets which were both in the leading position with respect to the eye movement trajectory ($F(1,6) = 1.31$, $p = .33$, $\eta_p^2 = .16$). Figure 15 shows the interaction effect.

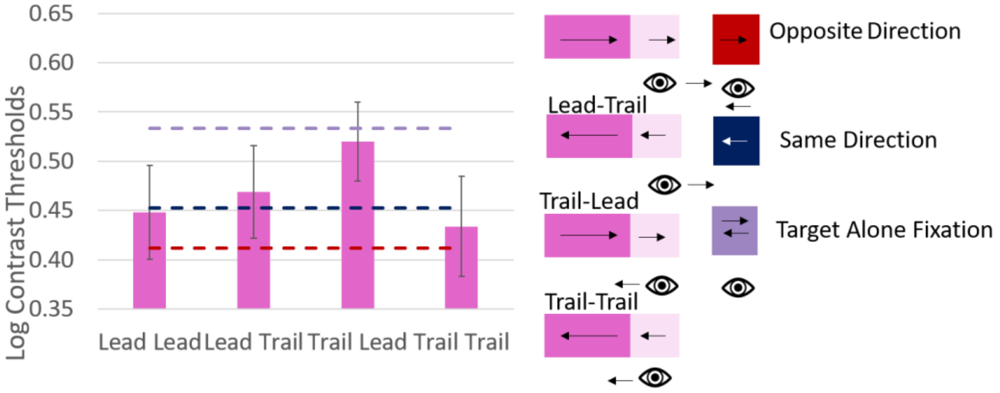


Figure 15. Overall results for isoluminant stimuli in Experiment 3A.

Log contrast thresholds are represented in the y-axis. On the x-axis, four different levels of the target’s position (Lead-Lead, Lead-Trail, Trail-Lead, and Trail-Trail) are shown. The first words represent the target’s position according to the eye movement trajectory. The second words represent the target’s position according to the drift direction. Red lines represent the baseline for the gratings, moving in the opposite direction with the eye movements. Blue lines represent the baseline for the gratings, moving in the same direction as the eye movements. Purple lines represent the baseline during fixation. Error bars indicate the standard errors of the mean (+/- 1 *SEM*).

For the luminance-defined chromatic stimuli, a three-way Repeated Measures ANOVA results revealed no significant main effect (all *p*’s > .05). There was a significant interaction for the phase difference and the position of the target with respect to the eye movement trajectory ($F(1,6) = 7.70$, $p = .03$, $\eta_p^2 = .56$). However, pairwise analyses revealed no significant difference for the log contrast thresholds across the conditions (all *p*’s > .05). Although it was not significant, as can be seen in Figure 16, the data pattern revealed an interesting interaction between the inducer position with respect to the eye movement trajectory and drift motion. Accordingly, the pattern revealed the opposite interaction observed with isoluminant gratings. The visibility of the target moving opposite to the eye movements and in the trailing position according to the object trajectory was smaller than the target moving the same direction with the eye movements and in the trailing position according to the object trajectory.

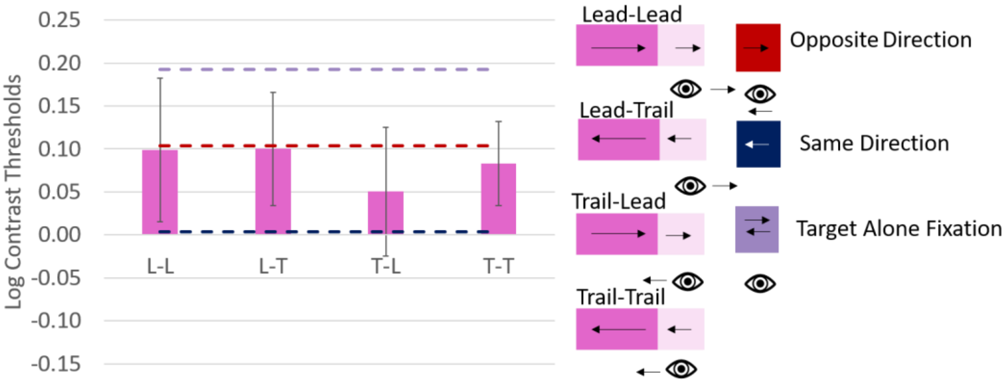


Figure 16. Overall results for luminance-defined chromatic gratings with 50% luminance contrast in Experiment 3A.

Log contrast thresholds are represented in the y-axis. On the x-axis, four different levels of the target's position (Lead-Lead, Lead-Trail, Trail-Lead and Trail-Trail) are shown. The first positions represent the target's position with respect to the object's trajectory. The second positions represent the target's position with respect to the drift direction. Red lines represent the baseline for the gratings, which were moving in the opposite direction with the eye movements. Blue lines represent the baseline for the gratings, which were moving in the same direction as the eye movements. Purple lines represent the baseline during fixation. Error bars indicate the standard errors of the mean (+/- 1 *SEM*).

3.3.5 Summary and Discussion

For isoluminant gratings, the results revealed that the visibility of the targets in the leading edge of the eye trajectory was higher than the targets in the trailing edge. However, the target's visibility in the trailing edge with respect to the drift direction was higher than the target's visibility in the leading edge. Moreover, there was a significant interaction between the target position with respect to the drift direction and the target's position on the eye movement trajectory. When the target was in the trailing position on the eye trajectory, the visibility of the target moving in the same direction as the eyes was higher than the target moving in the opposite direction as to the eyes. For luminance-defined chromatic gratings with 50%

luminance contrast, this effect reversed as a trend. The target's visibility moving in the opposite direction to the eyes was higher than the target moving in the same direction as the eyes if the targets were in the trailing position on the eye movement trajectory. We hypothesize that the allocation of spatial attention towards ahead of the eye movement trajectory during eye movements (Chen et al., 2017) could be responsible for this interaction. The spatial attention causes a shift in the visual receptive fields in cortical area MT (Womelsdorf, Anton Erxleben, Pieper, & Treue, 2006). Therefore, smooth pursuit eye movements can cause a shift or elongation of the extra-classical receptive fields of the cells towards the inducer grating for the targets in the trailing position. This shift towards the inducer gratings may suppress the visibility of the target by surround suppression mechanisms. Because the visual system boosts the contrast sensitivity of the isoluminant gratings moving in the opposite direction with the eyes, the suppression from the inducer moving in the opposite direction may be higher than the suppression from the inducer moving in the same direction. Further discussion on this issue will be provided in the General Discussion.

3.4 Experiment 3B

The results of Experiment 3A revealed a significant interaction for isoluminant stimuli between the target's position with respect the drift direction and eye movement trajectory. Accordingly, in conditions where the target was in the trailing position with respect to the eye movement trajectory, the target's visibility was suppressed if the target and the inducer had opposite drift direction with regards to the eye movement compared to the target that had the same drift direction as the eye movements. This effect was opposite to what we had found in Experiment 2.

Therefore, the presence of the inducer stimulus reversed the effect of smooth pursuit on the visibility of the target. We hypothesized that the presence of the inducer caused a suppressive effect on the target trailing the inducer on eye movement trajectory. Because the system is more sensitive to isoluminant stimuli moving in the opposite direction, the suppression effect was higher for the inducer with a drift direction opposite to the eye movements. To explore the mechanisms of this suppression effect, we manipulated the width of the inducer. If it was the surround suppression mechanisms that caused this suppression, then the suppression effect would get smaller as the width of the inducer gets thinner (Cannon & Fullenkamp, 1991).

3.4.1 Participants

Five of the seven observers participated in the experiment. Two of the participants were researchers involved in this study. The rest of the participants were naïve graduate and undergraduate students at Boğaziçi University. All participants participated in the experiments voluntarily and had normal or corrected to normal vision with no color blindness.

3.4.2 Stimulus

The stimulus for this experiment was kept the same as the stimulus configuration in Experiment 3A with only a few changes. Firstly, the width of the inducer was manipulated to see the changes in the suppression effect. In the experiment, two different width sizes were used. Firstly, the width of the inducer was reduced to 1 visual angle. Therefore, the overall size of the inducer was the same as the size of the target. Meanwhile, the width of the inducer was reduced to 0.5 visual angle where the inducer was smaller than the target. Secondly, Experiment 3B investigated the effect of inducer size only on the targets positioned at the trailing edge of the eye trajectory since the suppression effect was observed in the trailing edge. Therefore, the comparisons were made between the log-contrast thresholds of the targets that are in the trailing edge of the eye trajectory and drifting either the same or the opposite direction to the eye movements trajectories. Although there was no significant interaction for the luminance-defined chromatic stimuli in Experiment 3A, the data trend was similar to what we expected. Therefore, the effect of the inducer size was investigated for both isoluminant and luminance-defined chromatic stimuli with a %50 luminance difference between magenta and cyan signals.

3.4.3 Procedure

After calibration for the eye tracker in each block, participants initiated the experiment by pressing a key on the keyboard. The fixation appeared on the screen for 500ms after participants pressed a key on the keyboard. Participants kept their fixation at the fixation point throughout the experiment. After 500ms, drifting sinusoidal target and inducer gratings appeared on the screen and either moved horizontally or remained fixated for 2.6 seconds. Observers were asked to report whether the target grating appeared above or below the fixation point by pressing the up and down keys.

Participants completed two different blocks for each stimulus type and inducer size in random order. The blocks were containing the stimulus configurations of Trail-Trail and Trail Leading conditions. Each block had 140 trials. Participants first completed the blocks containing isoluminant stimuli with a random order of inducer size and moved on to complete the blocks containing luminance-defined chromatic stimuli with 50% luminance contrasts.

3.4.4 Results

For isoluminant stimuli, log-contrast thresholds of the conditions Trail-Trail and Trail-Lead were compared for each inducer size. For inducer sizes of 0.5° and 1°, the results of the paired-samples t-test revealed no differences between the two conditions (all *p's* > .5). To compare these two sizes with the original size (6.67°), the data from Experiment 3A with the same 5 participants who participated in Experiment 3B were examined using a paired-sample t-test. Log contrast thresholds of the conditions Trail-Trail, and Trail-Lead were different from each other (*t*(4) = 4.48, *p* = .01 *d* = 4.48), where the log-contrast threshold of the target drifting in the opposite direction to the eye movements (Trail-Lead) was higher (*M* = .50 *SEM* = .05) than the target drifting in the same direction as the eye movements (*M* = .41 *SEM* = .06). Figure 17 shows the results of the experiment.

For luminance-defined chromatic stimuli, the results of the paired-samples t-test revealed no difference between the conditions for 0.5° inducer size (*p* > .05). However, there was a significant difference between the log-contrast thresholds of two conditions for 1° inducer size (*t*(4) = 3.40, *p* = .03 *d* = 1.55). Again, to compare the data from Experiment 3A with the same 5 participants who participated in Experiment 3B were examined using a paired-sample t-test. There was no difference between the log-contrast threshold of the two conditions for the inducer size of 6.67° (*p* > .05). Figure 18 displays the results.

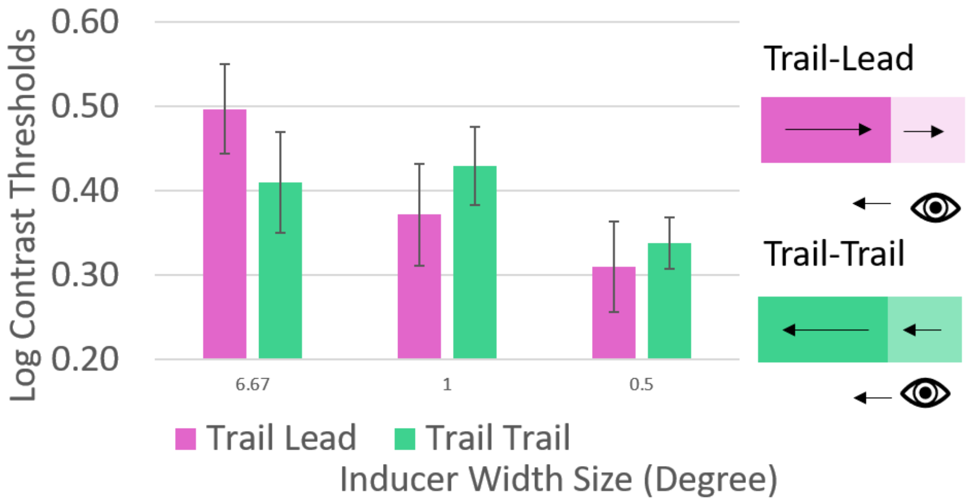


Figure 17. Overall results for isoluminant stimuli in Experiment 3B.

Log contrast thresholds are represented in the y-axis. On the x-axis, two different levels of the target's position (Trail-Lead and Trail-Trail) and three different inducer size conditions (0.5, 1, and 6.67 degrees) are shown. The first positions represent the target's position with respect to the object's trajectory. The second positions represent the target's position with respect to the drift direction. Error bars indicate the standard errors of the mean (+/- 1 *SEM*).

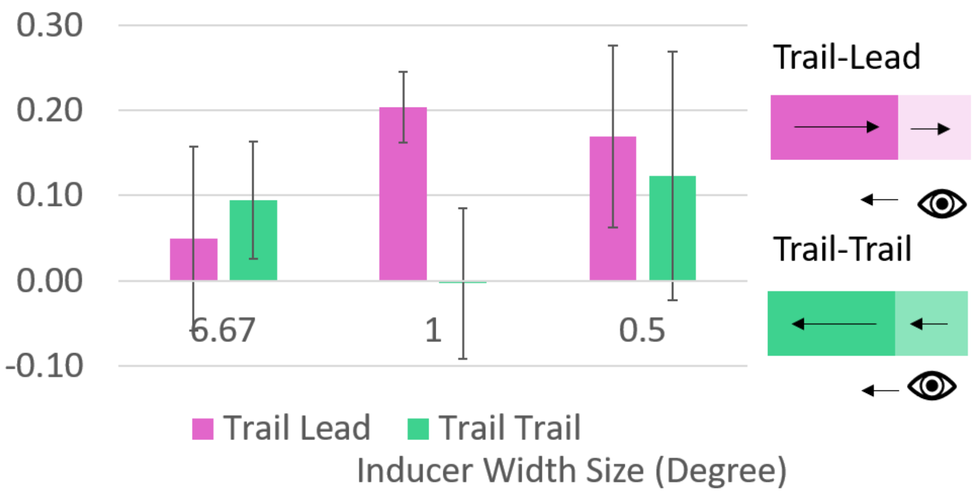


Figure 18. Overall results for luminance-defined chromatic gratings with 50% luminance contrast in Experiment 3B.

Log contrast thresholds are represented in the y-axis. On the x-axis, two different levels of the target's position (Trail-Lead and Trail-Trail) and three different inducer size conditions (0.5, 1, and 6.67 degrees) are shown. The first positions represent the target's position relative to the object's trajectory. The second positions represent the target's position relative to the drift direction. Error bars indicate the standard errors of the mean (+/- 1 *SEM*).

3.4.5 Summary and Discussion

The results revealed that for the isoluminant stimuli, the gradual decrease in the inducer’s size attenuated the inducer’s suppressive effect on the target in the trailing position relative to the eye trajectory and drifting opposite to the eye movements. On the other hand, for luminance-defined chromatic stimuli with 50% luminance contrast, the decrease of the inducer size for 6.67 visual angle to 1 visual angle facilitated the target’s visibility on the trailing edge of the eye trajectory moving in the same direction as the eyes. This facilitation effect disappeared when the inducer size was 0.5 visual angle. If surround suppression mechanisms caused a suppression, a decrease in the inducer size would decrease the suppression of the target’s visibility. In fact, as we expected, for isoluminant stimuli, the difference between the log contrast thresholds of the targets moving in the same and opposite direction with the eye movements disappeared as the inducer size decreased.

CHAPTER 4

GENERAL DISCUSSION

Overall, in this thesis, we investigated the contextual effects of motion and smooth pursuit eye movements on the visibility of chromatic gratings using the stimulus configuration introduced by Roach et al. (2001). Experiment 1 investigated the phase-dependent contrast sensitivity modulation using isoluminant and luminance-defined chromatic gratings during fixation. Experiments 3A and 3B investigated this modulation during smooth pursuit eye movements. Before investigating the effect of dynamic inducer grating on the visibility of the target grating during smooth pursuit, as a control study, Experiment 2 investigated the visibility of the drifting target grating in the absence of abutting inducer during smooth pursuit eye movements.

In the first experiment, we aimed to understand whether the phase modulation reported by Roach et al. (2011) and Arnold et al. (2014) occurs for isoluminant and luminance-defined chromatic gratings during fixation. Our experiment found the phase modulation effect at the trailing edge as a trend for isoluminant stimuli and as a significant effect for the luminance-defined chromatic gratings with 50% luminance contrast. Although it was not significant, the phase-dependent modulation at the trailing edge also persisted for the luminance-defined chromatic gratings with 100% luminance contrast. For both isoluminant and luminance-defined chromatic gratings with 50% luminance contrast, there was no phase modulation at the leading edge of the inducer. Moreover, we observed the phase modulation at the leading edge for the luminance-defined chromatic gratings with 100% luminance. In general, the presence of the inducer facilitated the visibility of the target for isoluminant and luminance-defined chromatic gratings with 50% luminance contrast. For luminance-defined chromatic gratings with 100% luminance contrast, the presence of inducer gratings suppressed the visibility of the targets with incongruent phases.

In a conference abstract, Hisekata et al. (2014) reported an investigation on the phase dependent contrast sensitivity using isoluminant inducer and target gratings with a paradigm similar to Roach et al. (2011). They reported that the contrast sensitivity for the target in the presence of the inducer is suppressed for isoluminant stimuli. Our results contradict Hisekata et al. (2014) in two main points. We observed a facilitation effect, rather than a suppression, in the presence of the inducer on the visibility of the target with isoluminant and luminance-defined chromatic gratings with 50% luminance contrast. Moreover, Hisekata et al. did not observe an asymmetric phase-dependent sensitivity modulation using isoluminant stimuli, either. Our results, on the other hand, demonstrated a phase-dependent sensitivity at the trailing edge of the inducer as a trend at isoluminance, which became significant with additive 50% luminance contrast. One difference our stimulus had from Hisakata et al. (2014) was the drift rate of the sinewave gratings. While Hisakata et al. (2014) used a drift speed of 5 deg/sec, our gratings drifted with a speed of 4 deg/sec. As Gegenfurtner and Hawken (1996) suggested, there are two different channels for chromatic motion: slow and fast. While the fast channel is more sensitive to speeds higher than 4 deg/sec, the slow channel is more sensitive to the color changes and speeds lower than 4 deg/sec. Thus, we think that the difference of our results from those in Hisekata et al. (2014) study could stem from the different channels' involvement in motion processing. The sensitivity of the slow motion channel is higher to changes in hue. Therefore, a disruption in the color pattern continuity may affect the motion induced sensitivity increasement for the stimuli processed by the slow channel. On the other hand, the fast motion channel is more sensitive to changes in luminance. Therefore, a disruption in the color pattern continuity may not affect the sensitivity to the target processed by the fast motion channel. Moreover, the suppression of the inducer on the visibility of target grating observed by Hisekata et al. (2014) could be explained by the fast channel's lack of ability to process motion signals from isoluminant stimuli (Gegenfurtner and Hawken, 1996). Thus, we argue that the enhancement of contrast sensitivity by motion signals might not be available for the stimulus processed by the fast channel in Hisekata's paradigm. Without the enhancement caused by the motion mechanisms, spatial mechanisms such as surround suppression (Wachtler et al.2003) could explain the observed suppressive effect of the inducer grating on the target's visibility.

Moreover, our results do not agree with the suggestion that the same phase-dependent spatial summation mechanism is responsible for the phase modulation observed in the leading and trailing edges of the inducer (Arnold et al., 2014). Our findings revealed that while the phase modulation at the leading edge depends on 100% luminance contrast for the inducer grating, the phase modulation at the trailing edge for chromatic stimuli does not have a gradual trend with the gradual increase in the luminance contrast. The psychophysical evidence shows that the size of the spatial summation area decreases with the increased luminance (Barlow 1958). Thus, suppose spatial summation occurs at the edges where the target and the inducer have congruent phases, we would expect to see a decrease in the phase modulation with increased luminance contrast. However, this was not the case neither for the leading nor for the trailing edges. In the trailing edge, 50% luminance contrast increased the phase dependency of the sensitivity. However, 100% luminance contrast decreased the phase modulation. For the leading edge, we observed the phase modulation only when the gratings were modulated with 100% luminance contrast. Therefore, spatial summation mechanisms failed to explain the observed phase modulation. We suggest that the lack of phase modulation at the leading edge may be explained by the motion-induced color-mixing effect where integration of chromatic signals along the motion trajectory occurs at the leading edge (Nishida et al., 2007). This integration of the color signals could make the phase dependency of the motion-induced sensitivity redundant at the leading edge since the cyan and magenta signals would get mixed and make the dependency to pattern continuation redundant for contrast sensitivity at the leading edge. Our results are not able to suggest a mechanism which leads to phase dependency at the trailing edges for isoluminant and luminance defined chromatic gratings with 50% contrast. On the other hand, they do show evidence for a mechanism which depends on luminance contrast for the phase modulation at the leading edge. One could argue that the facilitation effect we observed at the trailing edge could be caused by flank facilitation that occurs by the mere existence of surround stimuli (Polat & Sagi, 1993; 1994). However, it is known that for flank facilitation to occur the target and the flankers should have a certain spatial distance between each other (Polat & Sagi, 1993). Our phase modulation, on the other hand, occurred without a gap between the target and the inducer grating, eliminating the flanker facilitation based accounts.

Before investigating the sensitivity of abutting chromatic gratings during smooth pursuit eye movements, we examined this modulation when the target gratings were presented alone to better understand the contextual effects of inducer grating on the target's visibility during smooth pursuit eye movements. Therefore, Experiment 2 investigated the visibility of the drifting target grating during smooth pursuit. The experiments revealed that for isoluminant and luminance-defined chromatic stimuli with 50% luminance contrast, the eye movements facilitated the visibility of the target stimulus. However, the eye movements did not affect the luminance-defined chromatic target grating with 100% luminance contrast. Additionally, whereas for isoluminant target grating, the target drifting in the opposite direction to the eyes was more visible than the target drifting in the same way as the eyes as a trend, for luminance-defined chromatic stimuli with 50% and 100% luminance contrasts, the visibility of the target grating drifting in the same direction as eyes was higher than the target grating drifting in the opposite direction.

Schütz et al. (2008) reported a facilitation in the visibility of isoluminant stimuli during smooth pursuit eye movements. They argued that this facilitation is caused by a general boost in the parvocellular system to reduce motion blur caused by the eye movements. Here, we showed that the facilitation occurs not only for isoluminant stimuli but also for luminance-defined-chromatic gratings with 50% luminance contrast. On the other hand, the contrast sensitivities between the static eye and smooth pursuit conditions did not differ from each other with luminance defined-chromatic gratings with 100% luminance contrast. These results show that while the detection of chromatic signals improve during smooth pursuit, additive luminance signals introduce a destructive effect on the visibility of the target stimulus in the presence of eye movements. In fact, in line with this finding, Schütz et al. (2007a) and Schütz et al. (2007b) reported an attenuation of contrast sensitivity during smooth pursuit eye movements for achromatic stimulus. Both studies explained the attenuation of the achromatic contrast sensitivity with attentional processes since the target stimulus was presented in the periphery. Schütz et al. (2007a) and (2007b) suggested that during pursuit, contrast sensitivity to target in the periphery decreases because smooth pursuit and perception share the same attentional mechanisms (Khurana & Kowler, 1987) Visual attention increases the sensitivity to the target in the attentional spotlight (Carrasco, Penpeci-Talgar, & Eckstein, 2000). Therefore, without the allocation of full attention to the target stimuli, the sensitivity decreases during smooth pursuit compared to fixation. Our stimulus, on the other hand, was presented in the parafovea and was inside the potential attentional spotlight during smooth pursuit eye movements. Therefore, attentional mechanisms could not explain the destructive effect of additive luminance signals on the contrast sensitivity for chromatic stimuli. We propose that the attenuation of the contrast sensitivity for 100% luminance contrast can rather be explained by the increase in the TIRF of the visual system during smooth pursuit eye movements (Tong et al., 2009), where speeding up of TIRF reduces the sensitivity for luminance signals (Burr & Morrone, 1996). Moreover, we observed a directional selectivity for different luminance profiles. For isoluminant stimuli, the sensitivity to the target drifting in the opposite direction of eye movements was higher than the target drifting in the same direction as a trend. Contrast sensitivity being higher for the opposite drift in the isoluminant stimuli may reduce motion blur. If the visual system boosts the target's visibility (Schütz et al., 2008) moving in the opposite way of the pursuit (background motion), the signal-to-noise ratio would be lower for the objects in the background, which would lower the motion blur caused by the smooth pursuit eye movements. However, this directional selectivity changes with the additional luminance signals to the chromatic gratings. For both luminance-defined chromatic gratings, the sensitivity to the target drifting in the same direction of the eye movements was higher than the target drifting in the opposite way. Schütz et al. (2007b) reported a similar result where the visibility of the achromatic gratings drifting in the same direction with the eye movements was higher than the visibility of the achromatic gratings drifting in the opposite direction of the eye movements.

They explained this finding with feature-based attentional mechanisms where the attentional mechanism selects the visual target with the same directional properties as the eye movements. However, this could also be explained by the findings of Tong et al. (2009), where the TIRF for achromatic stimulus speeds up during smooth pursuit eye movements, especially for the targets drifting in the opposite direction. Because speeding up of the TIRF causes lowered contrast sensitivity for luminance signals (Burr & Morrone, 1996), the visibility of the luminance-defined chromatic targets drifting in the same direction ends up being higher than the targets drifting in the opposite direction. Therefore, we here see the interaction of the mechanisms caused by luminance and chromatic signals on the visibility of the target gratings during smooth pursuit eye movements. As mentioned in Experiment 1, the interaction of luminance and chromatic signals mostly occurs at area V1 and V2 (Mullen et al., 2015). However chromatic motion perception is suggested to be processed in the extrastriate cortex (Cropper & Wuerger, 2005; Gegenfurtner & Hawken, 1996), where separation of chromatic and luminance signals is observed more prominently (Mullen et al., 2015). Additionally, area MT is responsible for the initiation (Keller & Heinen, 1991) and area MST is responsible for the maintenance of the eye movements (Their & Ilg, 2005). Therefore, it may be argued that for a motion-induced directional selectivity on chromatic contrast sensitivity to occur during smooth pursuit, area V1 and V2 should receive a feedback from these extrastriate areas.

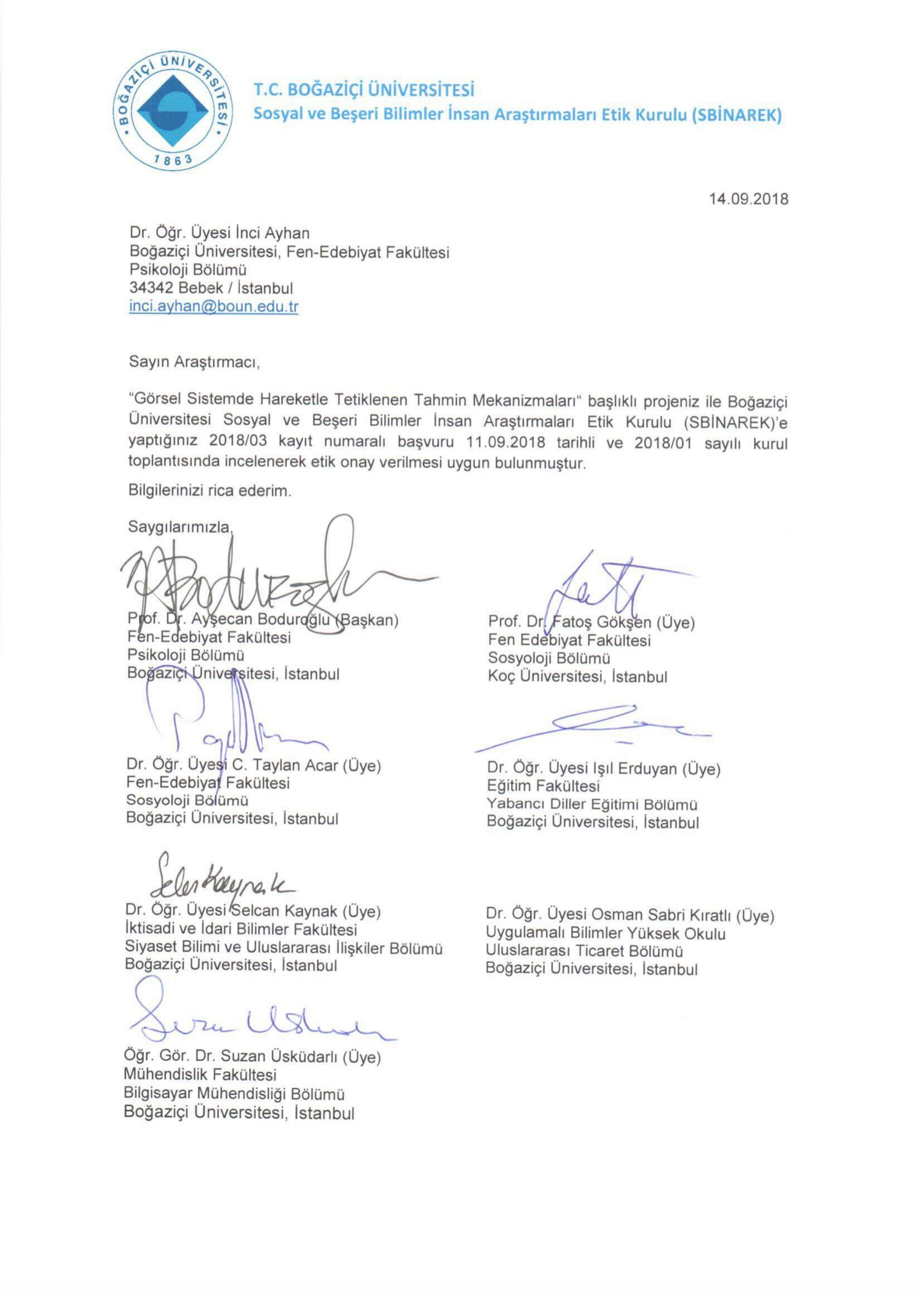
After discovering the phase-dependent motion modulation of the chromatic contrast sensitivity during fixation in Experiment 1 and directional selectivity of the chromatic contrast sensitivity during the smooth pursuit in Experiment 2, Experiment 3A aimed to understand the motion-induced contrast sensitivity changes during smooth pursuit eye movements for abutting chromatic gratings. We revealed a significant interaction between the smooth pursuit eye movements and the relative motion direction on the visibility of target gratings abutting the inducer grating for isoluminant stimuli. When the target gratings were in the trailing position on the eye trajectory, the visibility of the targets moving in the same direction as the eyes was higher than the targets moving in the opposite direction. For isoluminant gratings, we see that the visibility of the targets in the leading position with respect to the eye trajectory was higher than the visibility of the targets in the trailing position. Using the method of EEG frequency tagging, Chen, Valsecchi, and Gegenfurtner (2017) showed that the attentional allocation during smooth pursuit eye movements is slightly ahead of the fixation. This could be why the sensitivity for the targets in the leading position with respect to the eye movements was slightly higher than the targets in the trailing position. The spatial attentional mechanism causes a shift in the visual receptive fields in cortical area MT (Womelsdorf, Anton Erxleben, Pieper, & Treue, 2006). Therefore, for the targets in the trailing position, smooth pursuit eye movements could have caused a shift or elongation of the extra-classical receptive fields of the cells towards the inducer grating. This shift towards the inducer grating may have suppressed the visibility of the target by surround suppression mechanisms. This account could also explain why the target in the Trail-Lead (opposite direction) position was less visible than the target in the Trail-Trail (same direction) position. Experiment 2 showed us that the visual system is more sensitive to the gratings moving in the opposite direction of the eye movements for isoluminant gratings. Therefore, we would expect for contrast sensitivity of the system to be higher for the inducer grating drifting in the opposite direction to eye movements. This heightened sensitivity to the inducer grating, in turn, may increase the surround suppression mechanisms for the visibility of the target (Xing & Heeger, 2001). As a result, the masking effect for the target in the Trail-Lead position would be higher than the target in the Trail-Trail position. Although it was not significant, we see the results supporting this account for the luminance-defined chromatic grating with 50% luminance contrast. With luminance-defined chromatic gratings, the system's sensitivity was higher for the gratings moving in the same direction with the eye movements as we observed in Experiment 2. Therefore, the target's visibility in the Trail-Lead position would have to be higher than the target's visibility in the Trail-Trail position, as we observed empirically in our current data.

In Experiment 3B, as we expected, the effect of surround suppression on the target's visibility decreased with the decreasing inducer size for isoluminant stimuli. The target's visibility was higher in general for the targets in the Trail-Trail and Trail-Lead conditions as the inducer size decreased. Moreover, the difference between the log contrast thresholds for Trail-Trail and Trail-Lead conditions disappeared for the inducer sizes of 1° and 0.5° visual angles. These results support the account of surround suppression occurring for the targets in the trailing position with respect to the eye movement trajectory. For luminance-defined chromatic gratings, results revealed a complex interaction between the luminance signals and chromatic signals for the contextual effects of smooth pursuit eye movements. Although the difference between the Trail-Lead and Trail-Trail conditions was not significantly different for the inducer sizes of 6.67° and 0.5° visual angles, this difference became significant for the inducer size of 1 visual angle. The visibility of the target in the Trail-Lead condition decreased, and the visibility of the target in the Trail-Trail condition increased compared to 6.67° visual angle inducer size. This shows that different mechanisms come into play for the luminance-defined chromatic gratings when the inducer size was equal to the target size.

In general, in four different experiments, we showed that chromatic contrast sensitivity is affected by the motion of the surrounding stimuli, the execution of smooth pursuit eye movements, and the relative direction of the gratings' drift in relation to the eye movements' trajectory. Moreover, we showed that the visibility of the dynamic target gratings is affected by the interaction of chromatic and luminance signals during motion perception and smooth pursuit eye movements. It is known that the interaction between chromatic and luminance signals is processed in the early visual areas V1 and V2, whereas more selective processing is observed in extrastriate areas (Mullen et al., 2015). Therefore, we hypothesized that the effects we observed with an interaction of chromatic and luminance signals are processed in the early visual areas V1 and V2 with information coming through feedback mechanisms from higher extrastriate areas such as areas V3, V4, MT and MST. In Experiment 1, we showed that observed phase modulation in the trailing edge as a trend for isoluminant gratings became significant with additive 50% luminance contrast. 100% luminance contrast, on the other hand, did not increase the phase modulation at the trailing edge. Even though our results were not able to suggest a mechanism for the phase dependency at the trailing edge, we were able to eliminate spatial facilitation accounts caused by the static stimuli such as flank facilitation. Thus, we hypothesize that this modulation was rather induced by chromatic motion mechanisms. Chromatic motion is suggested to be processed at higher extrastriate areas (Cropper & Wuerger, 2005; Gegenfurtner & Hawken, 1996). If the interaction we observed between the luminance and chromatic signals at the trailing edge is processed at the early cortical areas (Mullen et al., 2015), then, we would expect higher cortical areas to feed information to the early cortical areas for the occurrence of phase modulation at the trailing edge. Moreover, in Experiment 2 we observed an interaction between luminance and chromatic signals on the directional selectivity of contrast sensitivity during smooth pursuit eye movements. This directional selectivity is hypothesized to stem from the change in TIRF of the system caused by the oculomotor signals. Extrastriate areas are responsible from the control and maintenance of the oculomotor signals (Keller & Heinen, 1991; Their & Ilg, 2005). Therefore, for this interaction between luminance and chromatic signals on directional selectivity to occur, extrastriate areas would be expected to feed information to early cortical areas where the interactions between luminance and chromatic signals are processed (Mullen et al., 2015).

APPENDIX A

ETHICS COMMITTEE APPROVAL



T.C. BOĞAZİÇİ ÜNİVERSİTESİ
Sosyal ve Beşeri Bilimler İnsan Araştırmaları Etik Kurulu (SBİNAREK)

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Sayın Araştırmacı,

“Görsel Sistemde Hareketle Tetiklenen Tahmin Mekanizmaları“ başlıklı projeniz ile Boğaziçi Üniversitesi Sosyal ve Beşeri Bilimler İnsan Araştırmaları Etik Kurulu (SBİNAREK)'e yaptığınız 2018/03 kayıt numaralı başvuru 11.09.2018 tarihli ve 2018/01 sayılı kurul toplantısında incelenerek etik onay verilmesi uygun bulunmuştur.

Bilgilerinizi rica ederim.

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See the footnote[1].

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[1] This thesis is a part of the project mentioned in the ethics committee approval form.

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