THE EFFECTS OF SMOOTH PURSUIT EYE MOVEMENTS AND ABUTTING PATTERN MOTION ON LUMINANCE CONTRAST SENSITIVITY

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ABSTRACT

The Effects of Smooth Pursuit Eye Movements and Abutting Pattern Motion on Luminance Contrast Sensitivity

Spatiotemporal context alters the visibility. The detectability of a low-contrast luminance-modulated sinusoidal target abutting a high-contrast drifting grating is impaired when the two stimuli are out-of-phase, suppression being strongest at the leading than at the trailing edge of motion. This effect was attributed to the predictive signals (Roach, 2011) or a spatial summation process and inhibitory motion deblurring occurring at the trailing edge (Arnold, 2014). In the previous studies, however, eyes were steady and the grating envelopes were stationary. It was shown that smooth pursuit eye movements influence the luminance sensitivity in a directionally selective manner. To gain a better understanding of the phase-dependent modulation of contrast sensitivity, I conducted a set of experiments, where the contextual modulation was investigated in the presence of smooth pursuit to examine the effects of pursuit velocity, directional congruence between the pursuit trajectory and the drifting gratings, and the contrast-dependency. Results indicated that the phase-dependent modulation occurs both at the leading and at the trailing edge under the fixation, although in different magnitudes contradicting the predictive model. During pursuit, the size of modulation at the leading edge depends both on the pursuit velocity and the directional congruency. Additionally, the magnitude of the modulation is contrast-dependent only at the leading edge. These findings are consistent with neither the predictive nor the spatial summation account but rather suggest different underlying mechanisms at the leading and trailing edges, which may be modulated by feedback connections from higher-order sensorimotor areas.

ÖZET

Yavaş İzleme Göz Takip Hareketlerinin ve Bitişik Hareket Örüntüsünün Luminans Kontrast Duyarlılığına Etkileri

Görsel bir uyaranın görünürlüğü uzam-zamansal bağlamdan etkilenmektedir. Yüksek kontrastlı sürüklenen ızgara uyaranına bitişik sinüs fonksiyonuyla tanımlı akromatik hedef uyaranın görünürlüğü iki uyaran farklı fazlarda olduğunda azalır. Bu baskılama, hedef uyaran harekete göre takip edenden ziyade yol gösteren konumunda olduğunda daha belirgindir. Kontrast duyarlılığının faza bağlı modülasyonu, öngörüsel sinyallere (Roach, 2011) veya uzamsal entegrasyona ek olarak takip edici konumda meydana gelen baskılayıcı mekanizmalara atfedilmiştir (Arnold 2014). Önceki çalışmalar bu etkiyi gözler sabitken ve ızgara uyaranlarını çevreleyen kontur durağanken araştırmıştır. Oysa göz takip hareketlerinin, görünürlüğü hareket yönüne bağlı bir şekilde etkilediği bilinmektedir. Bu tezde, göz takip, göz takip hızı, göz takip ve uyaran yönü arasındaki uyum ve kontrast bağımlılığının faz modülasyonu üzerindeki etkileri incelenmiştir. Sonuçlar, modülasyonun, gözler sabitken, öngörüsel model ile ters düşerek hem takip eden hem de yol gösteren pozisyonlarında fakat farklı büyüklüklerde gerçekleştiğini göstermiştir. Göz takibi sırasında yol gösteren konumundaki faz modülasyonunun büyüklüğü, uyaranların sürüklenme yönü ile görece göz takip yönü ve hızına bağlı değişmiştir. Ayrıca etki büyüklüğü, bitişik uyaranın kontrastına hedef uyaran yalnızca yol gösteren konumunda olduğunda bağlılık göstermektedir. Bu bulgular, öngörüsel model ve uzamsal entegrasyon açıklamaları ile ters düşmekte, yol gösteren ve takip eden konumlarındaki etkinin altında yatan mekanizmaların ayrı olduğunu ve duyu-motorsal alanlardan gelen geri beslemenin önemini göstermektedir.

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To my mom…

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LIST OF SYMBOLS AND ABBREVIATIONS

η_p^2	Partial eta-squared (as effect size)
^{o}	Degree (of visual angle)
cd	Candela
F	F-value of ANOVA
Hz	Hertz
M	Mean
ms	Milliseconds
N	Number of samples
p	Probability value
s	Seconds
SD	Standard deviation
t	t-value of a t-test
2AFC	Two-alternative forced choice (task)
ANOVA	Analysis of variance
CRT	Cathode ray tube
CRF	Classical receptive field
ERF	Extra-classical receptive field
FEF	Frontal eye fields
FPA	Frontal pursuit area
LGN	Lateral geniculate nucleus
MS	Means sum of squares
MST	Medial superior temporal area
MT	Middle temporal visual area, or V5

SE	Standard error
SEM	Standard error of the mean
TIRF	Temporal impulse response function
V1	Primary visual cortex, or striate cortex
V2	Secondary visual cortex, or prostrate cortex
V3	Third visual complex

CHAPTER 1

INTRODUCTION

The visual system does not operate in a way that aims to obtain a veridical representation of visual information but rather to functionalize the visual signals to produce adaptive behavior. For instance, visual illusions had been interpreted as a misperception and thought to result from spatial and temporal limitations of the visual system. Although this view is not false to some degree, accumulating behavioral and neuroimaging research has shown that the brain selects and processes sensory signals to infer useful information from them in order to successfully, or in better terms, adaptively interact with the environment (For a review, see Ayhan & Ünal, 2020). Thus, some visual illusions, or in a broader term, misperceptions, can be seen as a by-product of this strategy of the visual system. Similarly, an enhancement or impairment in visual sensitivity in some tasks might be an indicator of a functional organization and may be beneficial to understand and model neural mechanisms. The main focus of this thesis is to analyze how smooth pursuit eye movements interact with motion-induced contextual effects on luminance contrast sensitivity. First, I will present a brief overview of the visual system and psychophysical findings on the effects of smooth pursuit eye movements on visual perception and their possible functional roles. Secondly, I will give an overview of the literature on surround modulation at neuronal and perceptual levels. Finally, the related psychophysical and neurophysiological studies on motion trajectory and motion-induced contextual effects on contrast sensitivity will be reviewed.

1.1 Overview of motion processing in the visual system

Visual signals are transferred from retinal ganglion cells to the primary visual cortex (V1) through the lateral geniculate nucleus (LGN). There are four main types of ganglion cells in the retina (Dacey, 2004). Namely, these are midget, parasol, bistratified, and photosensitive ganglion cells. Midget ganglion cells have slow conduction velocity and smaller receptive fields and are sensitive to color (Dacey & Packer, 2003). They are also called P-cells since they project to the parvocellular layers of the LGN. As a result of having smaller receptive fields, P-type cells show high spatial acuity (Calkins, Schein, Tsukamoto, & Sterling, 1994). Parasol ganglion cells, on the other hand, have fast conduction velocity and larger receptive fields that make them have a poor spatial resolution, and they are not very sensitive to color (Watanabe & Rodieck, 1989). Because of receiving inputs from many rods and cones, this type of cell is sensitive to low contrast stimuli. Similar to the first letter connotation of P-type cells, parasol cells are also called M-type cells due to their projection to the magnocellular layers of the LGN. The third type of ganglion cell is bistratified cells which are sensitive to short wavelengths (Dacey, 1993). Both M-type and P-type cells have center-surround receptive fields, whereas bistratified cells have only a center receptive field with no surround (Dacey, 1999). Photosensitive ganglion cells contain melanopsin protein so that they are directly light-sensitive and project to the suprachiasmatic nucleus of the hypothalamus, which is responsible for controlling circadian rhythms (Do & Yau, 2010). In addition to the four types of ganglion cells, some retinal ganglion cells project to the superior colliculus, an area in the midbrain that controls eye movements (Perry & Cowey, 1984; Sparks, 1986).

As mentioned above, visual information from the retina is transferred to the visual cortex via two main distinct visual pathways through LGN. Magnocellular

pathway projects from parasol cells to two layers of the LGN, whereas parvocellular pathway projects midget cells' output to four layers of the LGN (Leventhal et al., 1981; Rodieck et al., 1985). Thus, neurons in magnocellular layers are color blind and more sensitive to high temporal and low spatial frequencies, and have transient responses (Kaplan & Sharpley, 1982). In contrast, parvocellular neurons are sensitive to color and high spatial frequencies and have sustained responses (Derrington & Lennie, 1984). Therefore, while the magnocellular pathway carries mainly motion-related information, the parvocellular pathway is important for object recognition. There is also a third pathway, koniocellular, formed by projections from bistratified retinal ganglion cells and located between magnocellular and parvocellular layers in the LGN.

The projections from magnocellular and parvocellular layers terminate in different sublayers of layer 4 of V1 (Hubel & Wiesel, 1972). Monocular and binocular neurons are also located at separate layers. V1 neurons are classified as simple or complex cells based on their receptive field properties (Hubel & Wiesel, 1962). Both simple and complex cells better respond to bars or edges and show orientation selectivity since their receptive fields show no center-surround organization in contrast to those of ganglion and LGN neurons but instead elongated in shape (Hubel & Wiesel, 1959). Furthermore, the receptive fields of simple cells consist of adjacent excitatory and inhibitory regions; thus, they show spatial phase sensitivity (Hubel & Wiesel, 1962). Complex cells, on the other hand, have no specific excitatory and inhibitory region and their preferred stimuli evoke a response at any location in their receptive field. This feature makes them spatially phase-invariant. However, recently it has been shown that their phase sensitivity increases at threshold level contrast, and this contrast-dependent phase sensitivity of V1

complex cells was not found for V2 complex cells (Crowder, van Kleef, Dreher, & Ibbotson, 2007; Cloherty & Ibbotson, 2015).

Directional selectivity, which is crucial to motion processing and controlling eye movements, emerges in V1 neurons in the macaque visual system. The receptive fields of some simple and complex cells are inseparable in space-time, meaning that the spatial organization of the receptive field does not remain the same over time (DeAngelis, Ohzawa, & Freeman, 1995). Together with the orientation tuning and space-time inseparable receptive fields, therefore, these simple V1 neurons prefer a particular direction to respond. Although high contrast stimuli evoke a larger response, directional selectivity was found to increase at low contrast (Peterson, Li, & Freeman, 2006).

According to the two-stream hypothesis, cortical visual information from V1 is processed and transmitted via two parallel and distinct streams which are thought to be extensions of subcortical magnocellular and parvocellular pathways (Mishkin & Ungerleider, 1982). Broadly speaking, the ventral stream is involved in the processing of features that are essential for object recognition like color, size, and form, whereas the dorsal stream processes information related to spatial vision and visually guided action. The receptive field sizes become larger, and tuning properties of neurons become more complex and specific as moving along the dorsal and ventral streams, respectively. Although it has been suggested previously that the two streams are functionally and anatomically distinct, accumulating evidence shows more complex connections and cross-talks between them through the visual hierarchy (Sheth & Young, 2016).

The middle temporal visual area (V5 or MT) is a part of the dorsal stream and responsible for motion processing. Its main inputs come from directionally selective

V1 neurons both directly or indirectly from some layers of V2 and V3. In addition to the cortical projections, MT also receives direct inputs from subcortical units such as koniocellular layers of the LGN and pulvinar (Sincich, Park, Wohlgemut, & Horton, 2004; Warner et al, 2015). Since area MT contains mostly direction-selective cells with larger receptive fields, ten times larger than those of V1 neurons, it is able to encode object motion by integrating local motion signals coming from direction-selective V1 cells into global motion together with V3A (Braddick et al., 2001). V3A is as sensitive to motion as MT (Bartels, Zeki, & Logothetis, 2008); however, it has been proposed that it responds only to external motion rather than retinal motion per se, unlike MT in humans (Fischer, Bulthoff, Logothesis, & Bartels, 2012). More recently, contrast-dependent phase sensitivity has also been found in macaque MT (Cloherty & Ibbotson, 2019). However, given that the observed phase sensitivity of V1 complex cells at threshold level contrast, this effect might be related to the projections from V1 (Cloherty & Ibbotson, 2015).

Another motion-related area is the medial superior temporal (MST), which is adjacent to MT. MST receives most of its inputs from MT and also contains heading-sensitive neurons implying its involvement in self-motion perception. Cells in MST have very large receptive fields covering most of the area in the visual field and can respond to more complex motions than those in MT like rotation and expansion/contraction. Therefore, these features make MST one of the main areas in optic flow processing (Lappe, 1996).

Apart from the dichotomy of the dorsal pathway which is dedicated to motion perception/action and the ventral pathway that is dedicated to object recognition, based on psychophysical and physiological findings, it has been proposed that there are at least two temporal channels for visual motion processing to detect local

motion, slow motion mechanism process slow velocities and color while fast mechanism process fast velocities and luminance (Gegenfurtner & Hawken, 1995,1996). For instance, the speed of a moving isoluminant chromatic object is perceived as slower than its physical speed (Cavanagh et al., 1984). These two motion channels are mediated by subcortical parvocellular and magnocellular pathways.

1.2 Smooth pursuit eye movements

We constantly move our eyes when exploring the outer world in order to bring the interested objects or area into the fovea. Eye movements are coarsely classified into two categories as saccadic (e.g., fast) and smooth pursuit (e.g. slow) eye movements. Either type of eye movement induces some instability in vision; however, stabilizing the tracked objects onto the retina is crucial to object recognition. For instance, visual sensitivity is reduced during saccadic eye movements, and therefore we do not perceive motion blur induced by retinal motion. This reduced sensitivity is called saccadic suppression and is thought to be accomplished by selectively suppressing the magnocellular pathway, which contains the primary inputs for motion processing (Burr, Morrone, & Ross 1994). Indeed, sensitivity for high spatial frequency and isoluminant objects is not affected at all or a little by saccades, given evidence for an intact parvocellular system which is more important for object recognition. Similarly, smooth pursuit eye movements have been linked to the parvocellular system but in a facilitative manner (Schütz, 2008).

Eye movements generate retinal motion in the direction opposite to the eye direction. This self-movement-induced motion is called reafferent motion, but we don’t usually perceive it (Wallach, Becklen, & Nitzberg, 1985). During pursuit,

stable world perception is achieved by integrating retinal motion signals induced by eye movements with efference copy signals generated by the motor command (Helmholtz, 1910; Holst & Mittelstaedt, 1950). Perceptual stability emerges late in the visual hierarchy since early visual areas encode the image in retinal coordinates (Gur & Nodderly, 1997; but see Guo & Li, 1997).

Smooth pursuit consists of two phases, one is an open-loop, initiation phase, and the other is a closed-loop or steady-state phase. Pursuit response is in the open-loop phase during approximately 140ms after the pursuit initiation (Lisberger et al.,1987). In this phase, pursuit response is modulated by only retinal motion since extraretinal signals are not ready for the visual system to inform about the eye velocity and help to reduce retinal slip. It has been proposed that smooth pursuit response is closer to motion perception during the open-loop phase; in fact, area MT is linked to pursuit initiation as revealed by TMS studies (Lisberger & Movshon, 1999). It has been shown that inhibition of MT activity results in the impairment of pursuit initiation, yet it has no primary influence on pursuit maintenance once the pursuit is initiated. Perceptual stability during the maintenance of pursuit requires matching the eye velocity with the velocity of the tracked object. However, eye velocity is generally smaller than target velocity, and a mismatch between eye and tracked object velocity induces retinal slip. Therefore, the retinal slip should also be taken into account for the pursuit compensation as well as reafferent motion cancellation. It has been shown that world-centered encoding of moving objects involves area MST, and neurons in MST also respond to eye velocity and retinal slip (Ilg, Schumann, & Thier, 2004).

1.2.1 Smooth pursuit effects on visual sensitivity and motion perception

Smooth pursuit and motion processing are closely linked and thought to share the same neural circuits to some extent (Krauzlis, 2004). Studies have mainly focused on how motion in the visual field influences smooth pursuit eye movement responses, pursuit initiation, maintenance, eye velocity, perturbations, position errors, etc. For instance, textured background moving in the direction opposite to pursuit causes decreased pursuit velocity (Masson, Proteau, & Mestre, 1995). However, pursuit performance enhances regardless of motion direction if a moving background does not cover the pursuit target trajectory (Spering & Gegenfurtner, 2007).

Our focus here is to study how smooth pursuit eye movements influence visual perception rather than contextual effects on pursuit response. Smooth pursuit can influence motion perception in several ways. For instance, stationary objects appear to move slightly in the opposite direction during pursuit, known as the Filehne illusion (Filehne, 1922; Freeman & Banks, 1998). This illusion implies a poor pursuit compensation to integrate retinal and extraretinal signals. It has been proposed that the perceived direction is modulated by the gain ratio of the eye movement and retinal signals, and perceptual errors in the direction domain result from a lower ratio of eye movement signal gain to retinal signal gain (Freeman, & Banks, 1998, Wertheim, 1994).

As another example, the perceived direction of vertical motion during horizontal pursuit depends on the stimulus duration and pursuit velocity (Souman, Hooge, & Wertheim, 2005). Souman et al. showed that the errors in the perceived direction decreased with increasing stimulus duration for higher pursuit velocities by using a single dot stimulus that was stationary in the horizontal dimension. Thus,

they argued that eye movement signal gain increases more than retinal signal gain with increasing duration and leads to better pursuit compensation.

Visual sensitivity is enhanced for isoluminant chromatic or luminance-defined gratings with high spatial frequency during smooth pursuit compared to steady-eye condition, although there are no facilitative or suppressive effects on luminance stimuli with low spatial frequency in the fovea (Schütz, 2008; Schütz, 2009; Braun, Schütz, & Gegenfurtner, 2017). For peripheral stimuli, smooth pursuit impairs the visibility of luminance stimuli (Schütz, 2008). All together, these findings were explained by the allocation of visual-spatial attention to the pursuit target (Schütz, 2007; Schütz, 2008). Since the maintenance of smooth pursuit requires attentional allocation on the tracked object, dividing spatial attention between the pursuit target and other objects causes reduced sensitivity for the untracked ones.

There is a significant body of research on the pursuit enhancement of visual perception of chromatic stimuli. Firstly, as mentioned above, Schütz and his colleagues (2008, 2009) studied smooth pursuit effects on visual sensitivity using contrast detection threshold experiments. In order to investigate the smooth pursuit effect per se, they used a briefly flashed line stimulus to eliminate retinal motion. Thus, their stimulus was both retinally and environmentally stationary. Their results showed that while contrast sensitivity for chromatic stimuli as well as for high-spatial frequency luminance stimuli and color-naming sensitivity (i.e., hue discrimination) increased during pursuit in comparison to fixation, contrast sensitivity for low spatial frequency luminance stimuli decreased in the periphery. These findings implied a parvocellular system-related enhancement. Moreover, their follow-up experiments indicated that improvement in sensitivity began 50ms before

the pursuit initiation. Furthermore, the pursuit enhancement increased with increasing pursuit velocity. Together with these results, the authors linked the increased visual sensitivity for chromatic and high-spatial frequency luminance stimuli to top-down extraretinal signals being responsible for boosting parvocellular activity and suggested MST and the frontal pursuit area of the FEF which feed information about the eye velocity as possible neural sites for boosting the parvocellular system. It has been proposed that the functional role of such a mechanism might be increasing sensorimotor gain, reducing motion blur or improving object recognition.

Given the findings of enhancement with increasing pursuit speed (Schütz, 2008) and stronger and faster eye movement response to small speed perturbations during pursuit (Tanaka & Lisberger, 2001; Tavassoli & Ringarch, 2009), it has been proposed that the aim of boosting slow-motion channel (i.e., parvocellular pathway) might be to improve sensitivity to changes in the tracked object's velocity to enhance tracking (Gegenfurtner, 2016). As a result, the increase in chromatic and high spatial frequency sensitivity would be a by-product of this process (Schütz, 2009). For further evidence, speed perception also improves for chromatic objects during pursuit (Braun et al., 2008). Another functional role of boosting the parvocellular system is to reduce motion blur induced by reafferent motion. Since motion blur is a more severe problem for chromatic and high spatial frequency stimuli due to temporal properties of parvocellular cells, it has been proposed that increased sensitivity for these types of stimuli might help to improve visual acuity and motion deblurring (Kelly, 1983; Schütz, Braun, & Gegenfurtner, 2009). Similarly, increasing sensitivity for chromatic and high spatial frequencies have also been suggested to be beneficial for recognition of the tracked object (Schütz, Braun, Kerzel, & Gegenfurtner, 2008).

1.2.2 Directional asymmetries in visual perception during SPEM and their functional roles

Both saccadic and smooth pursuit eye movements cause stationary background to move on the retina in the direction opposite to eye movement. Retinal image motion of stationary background opposite to pursuit provides information about the eye velocity and direction in addition to the extraretinal signals induced by eye movements. Thus, retinal motion in that direction carries more informative signals than the same direction as pursuit. Therefore, it is likely that different motion processing mechanisms could be performed by the visual system depending on the motion direction relative to the eye (Souto, Chudasama, Kerzel, & Johnston, 2019). It has been reported several perceptual asymmetries between the same and opposite direction, which were suggested to stem from different mechanisms with possibly different functional roles (Tong, Ramamurthy, Patel, Vu-Yu, and Bedell, 2009; Souto, Chudasama, Kerzel, & Johnston, 2019). Additionally, in reafferent motion, the response of direction-selective neuron populations in MT and MST has been suggested to be suppressed when their preferred direction is opposite to pursuit (Chukoskie & Movshon, 2009). Although MST is known to combine retinal motion and extra-retinal signals induced by pursuit and is sensitive to background motion (Ilg, Schumann, & Thier, 2004; Inaba et al., 2007**)**, more recently it has been suggested that V1 cells are also sensitive to gaze direction and encodes the stimuli in the real-world, as well as in the retinotopic coordinates (Morris & Krekelberg, 2019).

When carrier motion is opposite to pursuit direction, the perceived speed of the envelope motion decreases relative to the condition, where the carrier moves in the same direction as the eye, implying that perceived speed might be reduced due to catch-up saccades which have been strongly correlated with perceived speed changes

on a trial-by-trial basis **(**Hughes, 2018**)**. One might assume that reduction in perceived speed results from the impaired contrast sensitivity induced by catch-up saccades since low contrast objects are perceived as slower than high contrast ones (Spering et al., 2005). Indeed, as consistent with this idea, reduced contrast sensitivity for opposite direction was reported by some studies (Schütz et al., 2007; Tong et al., 2009). Schütz et al. measured temporal contrast sensitivity during steady state of pursuit. They showed that contrast thresholds are elevated for luminance-defined gratings drifting in the direction opposite to pursuit in comparison to the same direction. The authors proposed a feature-based attention account for reduced visual sensitivity for the opposite direction. In their study, contrast sensitivity for a low contrast peripheral grating target was slightly reduced during pursuit for the same direction in comparison to the fixation condition and the reduction in sensitivity was greater for the motion opposite to pursuit direction. They interpreted these results within the context of space-based attentional allocation to pursuit target and feature-based attention to pursuit direction, respectively. It is well known that attending a visual feature enhances the strength of neuronal response related to that feature (Martinez-Trujillo & Treue, 2004; Kamitani & Tong, 2006). Moreover, feature-based attentional modulation has been observed in multiple visual areas, including MT/V5 as well as early visual areas V1-V3 (Kamitani & Tong, 2006).

On the other hand, Tong et al. (2009) investigated directional asymmetries during pursuit by using achromatic gratings superimposed into the pursuit target. They found that smooth pursuit selectively influences contrast sensitivity such that contrast thresholds increase only in the opposite direction compared to the fixation. Although their findings were similar to those of Schütz and his colleagues (2007), the authors attributed impaired sensitivity for luminance stimuli to inhibitory motion

deblurring mechanisms, which are known to reduce gain in the magnocellular pathway. Additionally, they asserted that a cortical area must be involved to modulate the gain to achieve a directionally selective process.

Retinal motion can induce motion blur for the stationary objects in the background and it would be expected that motion blur increases with smooth pursuit eye movements due to the spatiotemporal variations added by the eye movements. However, reversed effects have also been reported (Bedell & Lott, 1996, Tong Aydin, & Bedell, 2007; Tong, Patel & Bedell, 2005). The extent of perceived motion blur is reduced during pursuit compared to fixation, and this effect is strongest for motion opposite to pursuit direction (Tong, Aydin, & Bedell, 2007). Thus, extraretinal signals may help to deblur motion, as Tong and colleagues suggested, via sharpening the temporal impulse response function, increasing the speed of visual processing. Temporal impulse response function (TIRF) indicates the visual system's response to impulse-like, brief stimuli. Faster TIRF results in reduced contrast sensitivity due to the lack of temporal summation for low-contrast stimuli. For example, TIRF becomes faster during saccades compared to fixation, implying the suppression of the magnocellular pathway to reduce motion blur induced by retinal motion during saccades and results in reduced luminance contrast sensitivity to reach a clearer percept (Burr & Morrone, 1996). Similar to saccades, smooth pursuit also influences the shape of TIRF, which speeds up during pursuit, especially for the stimuli moving opposite to pursuit (Tong et al., 2009). Although Tong and his colleagues have found a small difference between the natural frequency of TIRFs in fixation and motion opposite to pursuit, they argue that the difference would be larger for high-contrast stimuli because motion blur has been studied generally at high-contrast. Moreover, contrast sensitivity in the opposite direction decreased for

lower temporal frequencies, at around 4 and 6 Hz, while no increase in sensitivity was observed for high temporal frequencies.

For high contrast stimuli, the smooth pursuit can enhance motion processing in the direction opposite to the pursuit, and this enhancement in favor of the opposite direction is eliminated and sometimes reversed at low contrasts (Terao, Murakami & Nishida, 2015). Recently, Tereo, Murakami, and Nishida (2015) showed this directional bias using counterphase gratings. Counterphase grating consists of two gratings drifting opposite to each other at the same speed and results in no net motion on the retina under the fixation condition. In order to yield a counterphase stimulus during pursuit, Terao et al. (2015) came up with a paradigm, where one component grating was stationary and the other drifted in the same direction as pursuit but at a speed twice as fast as the pursuit target speed. This configuration ensured that both components drifted in opposite directions on the retina during the smooth pursuit. When a counterphase grating was presented in parallel to the pursuit target, the perceived direction was opposite to the pursuit direction. The authors suggest that the perceived direction of ambiguous retinal motion is dominated by the component grating drifting in the direction opposite to pursuit because of the enhancement of the motion signals in that direction due to smooth pursuit eye movements. They argued that the visual system has a preference for environmentally stationary or slower motion to obtain perceptual stability. This preference helps to segregate the pursuit target by assigning ambiguous retinal events to the stationary background.

Since stationary background moves in the opposite direction on the retina during pursuit, enhancing visual signals along the retinal motion trajectory helps to reduce motion blur induced by self-motion. Furthermore, a bias towards the retinal motion trajectory of stationary background might be useful to obtain more accurate

velocities of moving objects by using background pattern as a frame of reference since it covers most of the visual field. It should be noted that such a mechanism performs under supra-threshold conditions because motion blur is a more severe problem for high-contrast stimuli and impairing the visual sensitivity of high-contrast stimuli is not likely an effective way to reduce motion blur effects.

Another study related to the perceptual asymmetry between motion in the opposite and same directions as pursuit revealed that global motion processing is impaired when the direction of local motion signals is opposite to pursuit (Souto, Chudasama, Kerzel, & Johnston, 2019). Souto et al. argued that when the local motion direction is opposite to the pursuit, motion coherence thresholds are increased to extract global direction within the context of a different pattern of reflexive ocular tracking. Thus, the authors suggested that the motion integration mechanisms are differentiated for the motion in the opposite and same directions with respect to the eye movement. Since reafferent motion direction is dominant during pursuit, reducing the sampling area to compute global motion when motion is opposite to pursuit direction is an effective way to integrate local motion signals. On the other hand, reduced sampling leads to an impairment to perceive coherent motion, and extracting global motion direction becomes more problematic as coherence decreases.

Taken together, these studies overall suggest that the functional role or consequences of suggested mechanisms for directional selectivity helps to reduce motion blur induced by the self-motion. This is achieved by reducing magnocellular gain for opposite direction at low contrasts or integrating visual signals along the reafferent motion trajectory at high contrast.

1.3 Contextual interactions

Objects in natural vision are rarely isolated but rather surrounded by a context with both spatial and temporal components. Context influences the visual processing of a single stimulus in various ways and can alter the perception of basic stimulus features such as contrast, speed, and direction. In this section, I will first review neurophysiological findings on surround modulation obtained from single-cell studies in primates using drifting gratings to estimate the tuning properties of V1 neurons. Then I will mention psychophysical studies that reported suppressive or facilitative effects of surrounding contextual stimuli in focus on the effects of relative spatial phase between center and surround.

1.3.1 Surround modulation

Single-cell studies provided established evidence that the activity of a V1 neuron responding to a visual stimulus located in its receptive field can be modulated by another stimulus presented outside of its receptive field (Polat et al., 1998). This property is called extra-classical receptive fields (ERF), where a surrounding stimulus cannot evoke spiking activity in the absence of a central target but rather modulates the response presented in the classical receptive field. ERF modulation serves as a contextual component and is generally suppressive, leading to a reduction in the firing rate in V1 neurons (Silito & Jones, 1996; Walker, Ohzawa, & Freeman, 2000). It has been shown that surround modulation is spatially extensive such that a surrounding stimulus located up to 12.5 deg away from the center of the classical receptive field can modulate the neuron's response; however, the strength of the modulation gradually decreases as the distance increases (Shushruth, Ichida, Levitt,& Angelucci, 2009). Moreover, most suppressive modulatory effects are observed

when the surrounding and center stimuli have the same stimulus parameters such as orientation, spatial frequency, drift direction, and speed (Li & Li, 1994; Self etal., 2014; Henry et al., 2013). Therefore, it can be said that surround modulation has a tuned component. Furthermore, the tuning properties and the strength of suppression or facilitation in some cases depend on both surround and center contrast (Webb, Dhruv, Solomon, Tailby & Lennie, 2005). Surround modulation with high contrast surround is a binocular process and shows a narrow spatiotemporal tuning and orientation selectivity, while low contrast surround modulation is a monocular process and is more broadly tuned to stimulus parameters (Cavanaugh, Bair, & Movshon, 2002; Webb et al., 2005).

It has been proposed that feedforward, feedback, and lateral connections contribute to ERF modulation based on the spatial extent, tuning properties, and temporal dynamics of the observed surround effects (Angelucci & Bressloff, 2006). Feedforward and horizontal connections are both confined to near-surround modulation; however, while the former is untuned to orientation, the latter is orientation-selective and related to extracting object boundaries (Henry, et al., 2013; Shushruth et al., 2013). On the other hand, feedback connections from higher areas are involved in far surround modulation with a weaker orientation tuning and are thought to enhance visual saliency to drive attention (Angelucci et.al., 2002; Nurminen & Angelucci, 2014). For instance, optogenetic inactivation of feedback connections from V2 to V1 in marmoset brain increases receptive field sizes and therefore reduces response gain and surround suppression for near-surround and the proximal parts but not for the most distal parts of far-surround, similar to the visual spatial attention effects (Nurminen et al., 2018).

Despite extensive research on surround modulation, few single-cell studies reported the effects of relative spatial phase between surrounding and center stimuli. In one study, phase sensitivity on end- and side-inhibition have been investigated separately by recording the activity of V1 neurons of alert monkeys (Xu, Shen, & Li, 2005). They used drifting gratings and found that both regions exhibited relative phase sensitivity (RFS), and that simple and complex cells did not differ in terms of RFS. However, a cell showing suppression at the side regions is sensitive only to the relative phase of that region but not to the end-region. Moreover, the strength of suppression is strongly correlated with the relative phase sensitivity and introducing a 0.5-degree gap diminishes the phase sensitivity.

Another important aspect to consider physiological and behavioral results is the time course of stimuli exposure. A recent study revealed that ERF modulation on CRF response showed distinct spatiotemporal mechanisms in V1 as a function of duration (Henry et al., 2020). Using drifting annular surround, three distinct ERF mechanisms are suggested: tuned-facilitation, tuned-suppression, and untuned-suppression which take place at different time windows and exhibit different spatial extent. The two suppressive components are phase insensitive. The facilitative component of ERF, on the other hand, is orientation-tuned, and shows relative phase sensitivity in favor of in-phase configurations for collinear surrounds, which is maximal when the surrounding stimulus expands into CRF. Thus, facilitation would be explained by the integration of signals of high contrast surround and low contrast center within CRF. Although facilitation occurs for both simple and complex cells, only simple cells show phase sensitivity and more biphasic activity for the anti-phase (Henry et al., 2020). The time course of tuned facilitation is early, which peaks at intermediate durations between 60 and 120ms. Most of the neurons exhibiting tuned

facilitation also show untuned suppression at later phases, composing a biphasic activity. For longer stimulus durations, suppressive components dominate the response. Therefore, the time course of the stimulus and the spatial extent of the surrounding area has an effect on the ERF modulation and its phase sensitivity. Moreover, this study points out that in-phase facilitation likely results from the summation of inputs falling in the center of receptive fields.

Psychophysical findings are in line with the physiological findings on ERF modulation in V1 neurons. Surround suppression effects are strongest when the surrounding stimulus has the same orientation and spatial frequency as the center stimulus (Petrov, Carandini, & McKee, 2005). Iso-oriented suppression is also higher when the spatial phase of surround or edge stimuli is in-phase, aligned with the center's spatial phase with no gap in-between (Yu, Klein, & Levi, 2001). Behavioral studies investigating the effect of relative spatial phase between the center and surround on surround modulation, however, had used mainly collinear surround; thus, out-of-phase relationship could induce figure-ground segmentation, which can be explained by brightness induction (Ejima & Takahashi, 1985). In this case, brightness induction occurs due to the local edge contrast between center and surround. The dark bars of the surround are adjacent to the light bars of the center, and therefore the local luminance contrast between the two abutting opposite polarity bars results in an enhancement in the perceived contrast of the center. Indeed, many phase-dependent suppression effects were diminished by adding a small gap between center and surround, eliminating the local contrast signals (Xing & Heeger, 2001; Yu, Klein & Levi, 2001; Petrov & McKee, 2006). These studies suggest that phase-dependent effects might be driven by a highly localized separate mechanism rather than surround suppression. Additionally, surround suppression is contrast dependent

for an in-phase center, increasing with increasing surround contrast, while contrast changes in surround with an out-of-phase center are absent (Olzak & Laurinen, 1999).

Although surround effects are generally suppressive, an enhancement in perceived contrast in favor of in-phase had been observed only at configurations with low contrast surround and center (Ejima & Takahashi, 1985). Ejima and Takahashi (1985) have reported that the important factors in determining whether surround modulation is suppressive or facilitative are the relative phase and contrast of surround and center. They showed that when the contrast of the surround is lower than that of the center, the perceived contrast is increased in the in-phase condition for both horizontally and vertically surrounds. The apparent contrast of the out-of-phase center, on the other hand, does not depend on the relative or absolute contrast of the horizontally adjacent surround. Moreover, for vertically adjacent surrounds, the perceived contrast of the out-of-phase center increases with increasing surround contrast and does not depend on the relative contrast between the two. Taken together, these studies have shown that the phase-dependent surround modulation is observed in configurations, where there is no gap between the center and surround stimuli and is abolished by adding a small gap, implying very localized underlying mechanisms. Therefore, for the conditions that collinear surround is adjacent to the center, brightness induction has been suggested to account for the out-of-phase facilitation, whereas in-phase facilitation requires a low contrast center and surround configuration and can be explained by spatial summation mechanisms (Ejima & Takahashi, 1985; Yu, Klein & Levi, 2001).

Another contextual effect is called flank facilitation, which is shown to be phase-dependent and needs a small gap between target and flankers. In this effect,

the contrast sensitivity of a Gabor increases when presented with two or more co-aligned collinear Gabor patches called flankers (Polat & Sagi, 1993). Flanker studies have reported iso-oriented collinear flank facilitation effects in favor of in-phase alignments; the facilitation reduces for out-of-phase configurations (Solomon, Watson, & Morgan, 1999; Zenger & Sagi, 1996). Flank facilitation is also contrast-dependent; high contrast flankers improve the visibility of low contrast targets but have a suppressive effect on high contrast targets (Polat et al., 1998). Moreover, the facilitative effect of the flank strongly depends on the gap between target and flank, the ideal gap being approximately 0.24 visual degree and gradually decreasing with increasing gap and then saturating at further distances. Furthermore, flank facilitation also shows orientation and spatial frequency tuning like surround suppression and is thought to be important for perceptual grouping (Chen & Tyler, 2002). It has been proposed that long-range horizontal connections in V1 or elongated receptive fields contribute to flanker effects (Huang & Hess, 2008; Solomon, Watson, & Morgan, 1999).

1.3.2 Motion trajectory

When photons hit upon the retina, the light energy is converted into the electrochemical signals via phototransduction, which takes longer than auditory transduction (Fain, 2003). In addition to the sensory transduction, transmissions of visual signals through the visual hierarchy in the brain also take time. Consequently, these neural transmission delays produce a lag in the millisecond range between conscious percept and timing of the visual events. Thus, by the time we are conscious of a scenery, the environment has already changed in space-time. The lag between the percept and the physical present causes a problem, especially for

responding to time-varying events such as moving objects. Interacting with the dynamic world requires a precise timing of planned action and detecting the position of stimuli in space. Therefore, it has been proposed that the visual system compensates for the neural delays via predictive mechanisms such as predictive remapping of the visual field and extrapolation of motion trajectory (Nijhawan, 1994).

The localization of the objects is a fundamental task for the visual system and predicting the future position of a moving object is essential for action. Berry et al. demonstrated that the peak firing of retinal ganglion cells in salamander and rabbits is observed when their center of receptive field spans the area at or ahead of the leading edge of a moving object, indicating that the anticipation of the future position of a moving object begin at the early levels of visual processing (Berry, Brivanlou, Jordan, & Meister, 1999). Additionally, the motion onset also acts as an implicit cue to draw attention to the following trajectory. It therefore enhances the detectability of the trajectory embedded in noise, contributing to the prediction of future motion (Verghese & McKee, 2002). Thus, shifting the position of the moving object forwards along the motion trajectory might contribute to compensate for neural delays. Indeed, the perceived position of a stationary envelope carrying internal motion is shifted in the direction of the motion (De Valois & De Valois,1991). This perceptual phenomenon is called motion-induced position shift (MIPS) and has been widely studied psychophysically and neurophysiologically. Behavioral studies showed that the magnitude of MIPS depends on several stimuli-related factors such that longer presentation durations, higher speeds, and higher eccentricities, and lower contrast produce larger position shifts (Chung, Patel, Bedell, & Yilmaz, 2007; Kwon, Tadin, & Knill, 2015; Fu, 2004; Arnold, Thompson, & Johnston, 2007; Schnider et

al., 2019). Moreover, MIPS is larger when the stimulus has blurred edges rather than sharp edges (Fu, Shen, & Dan, 2001; Kwon, Tadin, & Knill, 2015).

It has been reported that the inward and outward motion or the leading and trailing edge of motion are linked to different neurophysiological activity patterns in the early visual areas (Whitney et al., 2003). These findings have been interpreted via accounts of cortical representation shift (Whitney et al., 2003), or predictability of motion (Maus, Weigelt, Nijhawan, & Muckli, 2010; Schellekens et al., 2016).

The retinotopic representation of the stimulus is slightly shifted in the direction opposite to the carrier motion in the early visual areas (Whitney et al., 2003; Schnider et al., 2019). These findings were interpreted as the flexibility of the visual field map such that the retinotopic representation of a moving object is modulated by motion direction. An fMRI study demonstrated that V3A shows higher activity for inward motion than for outward motion, which was interpreted as a predictive activity and an indication of a forward shift of the neuronal representation of the moving object (Maus, Weigelt, Nijhawan, & Muckli, 2010). Instead of a cortical representation shift, some studies suggested that the cortical map remains stable, but response amplitudes change, which might underlie the aforementioned differences (Liu, Ashida, Smith, & Wandell, 2006). Similarly, instead of or in addition to the shift in the retinotopic representation, higher activity in the early visual areas in response to the trailing edge of motion has been attributed to the inhibitory processes operating selectively at the trailing edge or to prediction errors which are thought to be caused by the novelty effect at the trailing edge (Whitney et al., 2003; Schellekens et al., 2016). According to the latter account, contrast changes at the leading edge can be predicted by the earlier visual information coming from the motion trajectory, while at the trailing edge, contrast changes are rather novel,

thus the unpredictability results in a higher BOLD response. Besides the difference in the hemodynamic activities, several behavioral studies also reported differences in the perceived contrast and contrast sensitivity between the leading and trailing edges (Whitney et al., 2003; Arnold, Thompson, & Johnston, 2007; Roach, McGraw, & Johnston, 2011; Arnold, Marinovic, & Whitney, 2014). Namely, reduced contrast sensitivity has been observed at the trailing edge compared to the leading edge. The decreased contrast sensitivity at the trailing edge also accounted for motion-induced position shifts (Whitney et al., 2003; Arnold, Thompson, & Johnston, 2007). According to this account, namely contrast modulation, the perceived position of a moving object is modulated by apparent contrast. Neurons which respond to the leading edge of motion become more active compared to those that respond to the trailing edge due to gain modulations, which in turn enhance the visibility of low contrast or blurred region. This account is also compatible with the higher BOLD responses at the trailing edge since inhibitory activities increase the blood flow but do not increase the spike rates (Mathiesen, Caesar, & Lauritzen, 2000).

1.3.3 Motion trajectory effects on phase-dependent contrast sensitivity

Roach and his colleagues (2011) have demonstrated a strong phase-dependent contrast modulation of contrast sensitivity at the leading edge of motion but not at the trailing edge. Their results showed that the contrast detection thresholds are lower when a low contrast target positioned at the leading edge of an abutting grating is in a spatiotemporal continuity with the abutting grating (i.e., in-phase) than when it is out-of-phase. This phase-dependent effect is observed only at the leading edge of motion rather than at the trailing edge. Roach et al. also showed that the observed phase effect is still present when the target and inducer grating are presented to

different eyes, indicating a cortical origin. In their paradigm, a small inter-stimulus gap (0.5 deg) was enough to trigger phase modulation at the leading edge, suggesting V1 as a likely locus, where neurons are known to have smaller receptive fields. Additionally, the phase difference effect was still present for brief durations as short as 50ms and increased with increasing duration, saturating at 500ms. Moreover, self-produced retinal motion (i.e., reafferent motion) via smooth pursuit eye movements was insufficient to induce phase-dependent change in contrast sensitivity.

Following these findings, Roach et al. proposed that the visual system can achieve this highly localized and spatial phase-dependent sensitivity modulation by employing a forward modeling. According to this model, based on the spatiotemporal pattern, an internal predictive signal is generated representing the expected future pattern of the stimulus ahead of the motion trajectory. As such, a hypothetical superposition of the predictive signal with the sensory signal would either facilitate or interfere with the visibility. If the sensory signal is congruent with the predictive signal, their sum would lead to an increase in the visibility of the visual input when the target is in-phase with the inducer. Conversely, when the target and inducer are out-of-phase, the superposition of the predictive and sensory signal would form a destructive interference, resulting in a drop in the target detectability. In this context, constructive interference would help to reduce the detrimental effects of the surround suppression and improve the sensitivity along the predictable motion trajectory.

Using the same experimental design and stimulus characteristics, Arnold et al. (2014), however, reported a phase-dependent modulation in the contrast sensitivity at the trailing, as well as at the leading edge, although in a smaller yet significant magnitude. They also showed that this phase-dependent modulation is

present in a flicker paradigm, in the absence of any directional motion and at the sides, as well as at the leading and trailing edges of the inducer motion. The phase modulation was absent when the luminance of a luminance-defined first-order stimulus was summed to grey across a small retinal area. These results together were inconsistent with the idea of a forward model which generates perceptually explicit predictive signals in the direction of the motion trajectory. Moreover, the authors suggested that the non-predictive spatial summation of signals spanning the boundary between the target and inducer grating at both leading and trailing edge and additional suppressive signals for motion deblurring that reduced the magnitude of the effect at the trailing edge. Arnold et al., however, have not elaborated the proposed mechanism for the non-predictive phase-sensitive spatial summation except that they suggested V1 simple cells as possible neural loci. It should be noted that their attribution of the reduction in the phase modulation at the trailing edge to the inhibitory motion deblurring process also depends on their findings, which demonstrated higher contrast sensitivity at the leading edge compared to the trailing edge in the in-phase condition.

According to the predictive model, the superposition of the predictive signal formed by a high spatial frequency inducer and the sensory signal of a low-frequency target should result in a destructive interference for both in-phase and antiphase targets. However, it has been reported that the phase-dependent modulation is tuned to the absolute spatial frequency of the target rather than to the relative spatial frequency between the target and the inducer (Chambers & Roach, 2014). The phase-dependent modulation was also observed when the spatial frequency of the inducer is varied, while the spatial frequency of the target is fixed to 1 degree per angle, which challenged the spatial summation explanation based on the properties of phase-

sensitive V1 simple cells (Chambers & Roach, 2014). In Chambers and Roach's (2014) study, the spatial frequencies of the inducer exceeded the average bandwidth of a simple cell tuned to the spatial frequency of the target (1 c/deg) (Chambers & Roach, 2014; Chambers, 2016; De Valois, Albrecht & Thorell, 1982). Since spatial summation is known to occur when the two stimuli are close in spatial frequency, a summation of the responses of simple cells which have receptive fields positioned across target and inducer is an unlikely explanation for the phase-dependent modulation observed at different relative spatial frequencies of the target and inducer.

1.4 Motivation

Previous studies on the phase-dependent modulation of contrast sensitivity along the motion trajectory investigated this effect when the eyes were fixated, and the envelope was stationary (Roach, McGraw, & Johnston, 2011; Arnold, Marinovic, & Whitney, 2014; Chambers, 2016). However, in daily life, we constantly move our eyes and track dynamic objects using smooth pursuit eye movements. Given the findings on the directionally selective visual processing during the smooth pursuit, the main aim of the present study is to elucidate the potential mechanisms underlying the phase modulation with the interaction of smooth pursuit eye movements.

To gain a better understanding of the phase-dependent modulation of contrast sensitivity, firstly, an experiment similar to the main experiments of Roach and Arnold's studies was conducted (Study 1A). Our data was similar to the findings of Arnold et al. such that the phase-dependent modulation of contrast sensitivity occurred at the trailing, as well as at the leading edge but in a smaller magnitude. However, in contrast to Arnold et al.'s results, we did not find any difference in the

contrast sensitivity for the in-phase targets at leading and the trailing edges of motion. This finding is in contradiction to the spatial summation account. In order to determine whether the first-order luminance-based motion mechanism regulates the observed phase modulation, the same experiment was repeated using second-order motion stimuli (Study 1B). Roach et al. had also investigated the phase-dependent effect using second-order motion and found a null result; however, they had measured contrast sensitivity only at the leading edge of motion, whereas in this thesis, we studied the contrast sensitivity at the trailing as well as at the leading edge.

Secondly, we investigated how smooth pursuit eye movements interact with the contextual effects on contrast sensitivity and phase-dependent modulation (Study 1C). The contextual effects here refer to whether the direction of the carrier motion is in the same or opposite to pursuit trajectory. The main results showed that the contrast sensitivity is lower when the internal (carrier) motion of the target is in the opposite direction to pursuit than when it is in the same direction. Moreover, directional incongruency also reduces phase-dependent modulation mainly at the leading edge. Study 1D aimed at investigating the effects of smooth pursuit eye movements on surround suppression and its phase-dependency on static gratings with moving envelopes. Following this experiment, we studied whether directionally selective effects on contrast and phase sensitivity during the smooth pursuit are also pursuit velocity dependent. (Study 2). Finally, to explore the contrast-dependency of phase-dependent modulation, Study1A was repeated with low inducer contrast in order to test the spatial summation account (Study 3).

CHAPTER 2

GENERAL METHODOLOGY

2.1 Participants

Participants were mostly affiliated with the Boğaziçi University Vision Laboratory and participated in the experiments on a voluntary basis without any incentive or course credits. All participants had normal or corrected-to-normal visual acuity. The number of participants corresponding to the various sets of experiments were 10, 5, 10, 5, 6, and 4 for Experiment 1A, 1B, 1C-D, 2, 3, and 4, respectively. The experimental protocol was approved by the Boğaziçi University Ethics Coordinating Committee (see Appendix A). Most of the participants were naïve to the aim of the experiments except for the four observers including the author and one of the supervisors. The data was saved with the initials of the names to ensure the anonymity and confidentiality of the participants. Since all participants were native Turkish speakers, experimental instructions and the informed consent forms were given in Turkish.

2.2 Stimuli and apparatus

The experimental setup consisted of an HP ProDesk 400 G3 Business PC desktop and a CRT monitor (Philips 109B40/20) with 1280x1024 pixels resolution and 75 Hz refresh rate. The monitor was calibrated using a Datacolor Spyder4Elite Colorimeter. 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. Stimuli were generated and displayed using MATLAB with Psychtoolbox-3 (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007). Additionally, a Bits# Stimulus

Processor (Cambridge Research Systems, Rochester, Kent, England, 2002) with 14-bit resolution controlled by MATLAB was connected to the Monitor to obtain a high grayscale resolution, enabling to test the contrast thresholds accurately. The maximum and minimum luminance values of the screen were 65.6 cd/m² and 0.002 cd/m², respectively. The monitor output was gamma-corrected (Gamma = 2.2) using the PTB function PsychColorCorrection('SetEncodingGamma') in each experimental session. All experiments were run in a dark (i.e. < 0.5 cd/m²) and quiet cubicle in the Boğaziçi University Vision Laboratory. A fixed chair and a chin-rest with forehead support were used to control the viewing distance of 57 cm. At this distance, one cm on the screen corresponded to one visual angle.

In all experiments, except in Experiment 1B, were used vertically oriented, luminance-modulated achromatic sinusoidal gratings, whereas in Experiment 1B were used contrast-modulated sinusoidal gratings. Contrasts of luminance-modulated gratings were defined by the Michelson formula, $(L_{max} - L_{min}) / (L_{max} + L_{min})$, where L_{max} is the luminance value of the brighter and L_{min} is the luminance value of the darker phase of the sinusoidal grating.

2.3 Procedure

At the beginning of each experimental session, the procedure started with the verbal instructions and the eye tracker calibration. The study consisted of contrast detection threshold experiments with the method of constant stimuli within a two-alternative forced-choice paradigm, and responses were collected via a common keyboard. No feedback indicating the correctness of the response was given. A typical session lasted approximately 20 minutes.

2.4 Data analysis

To obtain individual contrast detection thresholds, cumulative gaussian functions were fitted to individual distributions of correct responses at each contrast level using the psignifit toolbox version 2.5.6 for MATLAB (Wichmann & Hill, 2001). The seven stimulus levels were log-transformed Michelson contrasts (i.e. log of the percentage with a base of 10, for instance, %100 contrast corresponds to 2 log value) for the fitting. Contrast detection thresholds were yielded by taking the point estimate at which observers could detect the target gratings on 75% of the trials. All statistical analyses were performed with Repeated Measures ANOVAs with multiple factors or paired sample t-tests using IBM SPSS Statistics.

2.5 Eye movement recording and analysis

The display was viewed binocularly. All analyses were done offline and by manual coding due to the lack of software support. No filter was applied to the eye position and the velocity signals since the sampling rate was low (i.e. 30 Hz). To detect saccades, we used a cut-off criterion (95,000 $^{o}/s^{3}$) on the third derivate of eye position called jerk (Wyatt, 1998). if two consecutive samples of jerks exceeded the criterion, it was assumed that the corresponding time interval involves a saccade. If just one sample exceeded the criterion, the eye position signal causing the deviation was removed and replaced by an interpolative approximation using the nearest two samples. Trails containing a saccade after the 300ms of the motion onset of the pursuit target were discarded. Pursuit intervals were defined as the intervals that the eye position did not deviate from +/- 3º of the position of pursuit target at x-axis during at least 700ms between the time pursuit target started to move and the following 1100ms. We obtained eye velocity signals by computing the two-point

forward difference differentiation algorithm over the interpolated samples in the time intervals detected as a pursuit. Pursuit gain was calculated as the average eye velocity in the pursuit intervals divided by target velocity. Trails containing a sufficiently long pursuit interval and a pursuit gain lower than 1.5 were considered valid. Although we kept the criterions very large to compensate for the low sampling rate and the internal noise of the eye tracker, a significant number of trials were classified as invalid resulting from the pursuit gain criterion, indicating further smoothing may be required. For these reasons, the results obtained from the subjects whose data contained a sufficient number of valid trials in each condition were compared with the trends in the whole data without discarding any trial.

CHAPTER 3

EXPERIMENTS

3.1 Experiment 1A: Phase-dependent effects of the abutting pattern motion during fixation

Roach et al. (2011) demonstrated that when a low contrast target was presented with a high contrast abutting grating, the detectability of the target was dependent on the relative phase between the two stimuli only at the leading edge of motion. On the other hand, Arnold et al. (2014) showed that the phase-dependent effects on contrast sensitivity was also present at the trailing edge but was reduced in magnitude. Arnold et al. (2014) have attributed the reduced phase-dependent modulation to an inhibitory motion deblurring process at the trailing edge. Due to the discrepant findings between the studies of Roach et al. (2011) and Arnold et al. (2014) and the within-subject design nature of the current study, a similar experiment was conducted to explore the phase-dependent modulation of contrast sensitivity at both leading and trailing edges of motion when the eyes were fixated, and the grating envelopes were stationary.

3.1.1 Methods

Ten observers participated in Experiment 1A. Six of them were naïve participants. All observers had a normal and corrected-to-normal vision. The target stimulus was a low contrast sinusoidal grating (width and height = 1º, spatial frequency = 1 c/°), presented 1.5º below or above the fixation (randomized across trials). Two drifting sinusoidal gratings (inducers; width=6.67º, height = 1º, spatial frequency = 1 c/°) with 100% Michelson contrast were positioned so as to abut the target and its correspondent region on the opposite side (Figure 1). Both the inducer and the target

gratings drifted in the same direction at a speed of 5º/sec. That the target would be at the trailing or at the leading edge of the inducer was determined by the drift direction of the inducer grating in each trial. For instance, when the inducer gratings appeared on the left side, the leading condition corresponded to the case, where the drift directions of the inducer and the target were from leftwards towards rightwards.

Each trial began with the presentation of a central fixation point (a light gray dot) for 500ms. By the end of the 500ms period, both the inducer and the target gratings appeared on the screen for 2100ms. The task of the observers was to indicate whether the target stimulus appeared above or below the fixation via a keypress using the up or down keys. The spatial phases of the inducer and the target were randomized across trials. The sinusoidal waveform of the target was either in-phase (0° shift) or out-of-phase (180° shift) with the inducer's waveform. The relative phase conditions were presented at blocked trials. In the baseline condition, the target was presented in the absence of the inducer. One block of trials took approximately 20 minutes, and observers completed three experimental sessions in random order.

Contrast thresholds were obtained using the method of constant stimuli, with the presentation of each of the seven equally log-spaced contrast levels for 20 trials. The data fitting procedure was detailed in the General Methods section.

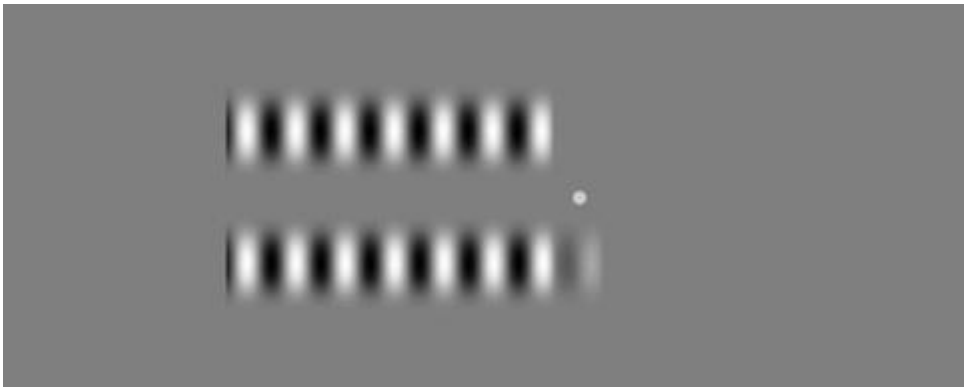


Figure 1. Stimulus configuration

3.1.2 Results

To examine the effect of the target position (leading edge and trailing edge) and the relative phase between the target and the inducer (in-phase and out-of-phase) on contrast sensitivity, a 2x2 Repeated Measures ANOVA was conducted. This analysis revealed significant main effects of both relative phase ($F(1,9) = 46.46$, $p < .001$, $\eta_p^2 = .84$) and target position ($F(1,9) = 8.38$, $p = .018$, $\eta_p^2 = .49$). Interaction between the target position and the relative phase was also found to be significant ($F(1,9) = 8.47$, $p = .017$, $\eta_p^2 = .49$). The simple main effect of relative phase was significant for both at the leading ($F(1,9) = 56.99$, $p < .001$, $np^2 = .86$) and at the trailing edge ($F(1, 9) = 23.93$, $p = .001$, $\eta_p^2 = .73$). In consistent with the significant interaction, whereas contrast thresholds were lower at the trailing edge ($F(1,9) = 10.06$, $p = .011$, $\eta_p^2 = .53$) than in the leading edge when the inducer and the target were out-of-phase, in the in-phase thresholds the thresholds were not differentiated between the trailing and the leading edges ($F(1,9) = .47$, $p = .513$, $\eta_p^2 = .05$). Moreover, as shown in Figure 2, in the presence of inducers, contrast thresholds with respect to the baseline condition were elevated only in the out-of-phase conditions.

The effect of target position (leading vs. trailing) on the phase-dependent modulation of contrast sensitivity were further examined by running a paired samples t-test on the difference between the out-of-phase and in-phase thresholds. This revealed that the phase-dependent modulation at the leading edge ($M = 1.31$, $SD = .55$) was greater than that at the trailing edge ($M = .88$, $SD = .60$), $t(9) = 2.91$, $p = 0.017$.

These results demonstrate that the phase-dependent modulation of contrast sensitivity occurs both at the leading and at the trailing edges but in different magnitudes. To be more specific, contrast sensitivity at the leading edge of the

motion trajectory relies more on the relative phase between the target and inducer than that at the trailing edge, as illustrated in Figure 2B. The reduction in the contrast sensitivity caused by the out-of-phase inducer grating was greater at the leading edge than at the trailing edge. Overall, these findings supported neither the predictive model (Roach, McGraw, & Johnston, 2011) nor the spatial summation account (Arnold, Marinovic, & Whitney, 2014). Although the phase-dependent modulation was stronger at the leading edge, there was still a significant effect of relative phase at the trailing edge, contradicting the predictive model.

According to Arnold et al. (2014), the inhibitory activity of the motion deblurring occurring at the trailing edge of motion reduces the phase-dependent modulation. If that is the case, then this suppressive process would also reduce the contrast sensitivity at the trailing edge when the sinusoidal waveform of the target is in-phase with the inducer. In contrast to the findings of Roach et al. (2011) and Arnold et al. (2014), however, this effect was absent in our data such that there was no difference in the contrast thresholds between the leading and the trailing edge in the in-phase condition. Moreover, any inhibitory process would also elevate the contrast thresholds at the trailing edge above the baseline, which is not the case as shown in Figure 2. Therefore, these results suggest that the reduced phase-dependent modulation at the trailing edge does not result from a directionally selective inhibitory process.

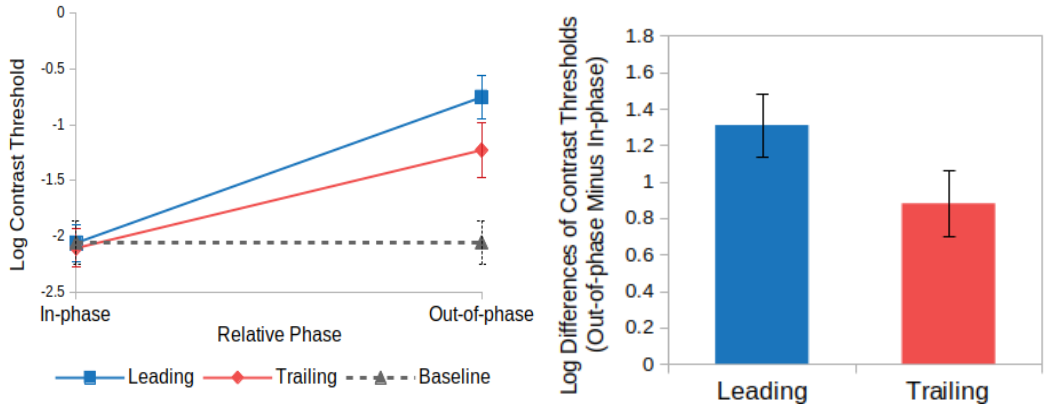


Figure 2. Overall results of Experiment 1A

A) The phase-dependent modulation of contrast sensitivity for the target positioned at the trailing (red line) and leading (blue line) edges of motion. Contrast thresholds are plotted as a function of the relative phase. The dashed lines represent the baseline (no inducer) condition. B) Mean differences between out-of-phase and in-phase contrast thresholds. Error bars indicate +/- 1 SEM.

3.2 Experiment 1B: Phase-dependent effects of the abutting pattern for second-order motion

To investigate whether the observed phase-dependent modulation of contrast sensitivity is present for the second-order motion, as well as the first-order motion, Experiment 1A was repeated using luminance-modulated sinusoidal gratings both at the leading and trailing edges during fixation. If the phase-dependent effects were regulated only by the first-order motion mechanisms, which detect the local shifts in luminance (Lu & Sperling, 1995), then we would observe the phase modulation neither at the leading nor at the trailing edges in this experiment.

3.2.1 Methods

5 observers who participated in Experiment 1A were also tested in Experiment 1B. Two of them were naïve to the aim of the experiment. Random 2-D binary static noise patterns modulated by contrast-defined, vertically oriented sinusoidal grating were used as the second-order stimuli. The inducer gratings (6.67º width, 1º height,

spatial frequency = 0.5 c/°) had a Michelson contrast modulation of 80% and drifted at a speed of 3 °/sec . The target grating (width = 2º (one full cycle), height=1º, spatial frequency = 0.5 c/°) drifted always in the same direction as the inducer gratings (3 °/sec). The background was also comprised of binary static noise. The experimental procedure was the same as in Experiment 1A. Observers completed two blocks, either in-phase or out-of-phase condition in a random order. Leading and trailing conditions were presented in the same block of trials.

3.2.2 Results

We conducted a 2x2 Repeated Measures ANOVA on contrast thresholds with two main factors, target position (leading edge and trailing edge) and relative phase (in-phase and out-of-phase). The analysis showed that neither the main effects of target position ($F(1,4) = 2.24$, $p = .209$, $\eta_p^2 = .36$), and the relative phase ($F(1,4) = .09$, $p = .775$, $\eta_p^2 = .02$), nor the interaction ($F(1,4) = .42$, $p = .552$, $\eta_p^2 = .10$) were significant. As shown in Figure 3, the phase-dependent modulation of contrast sensitivity was absent for the second-order motion both at the leading and at the trailing edges. These results indicate that luminance-based motion requires to induce a phase-dependent modulation both at the trailing and leading edges of motion.

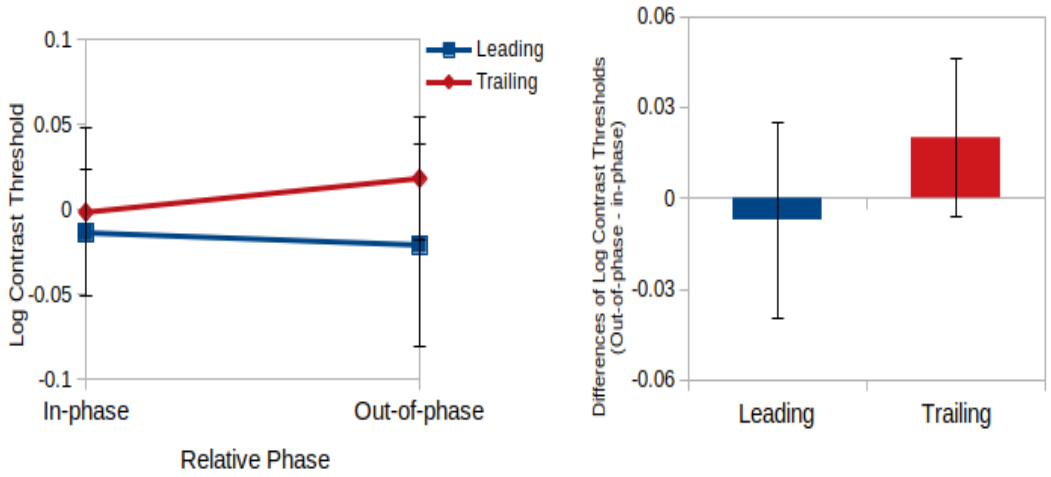


Figure 3. Overall results of Experiment 1B

A) Mean contrast thresholds are plotted as a function of the relative phase between the target and the inducer gratings. The blue line represents the leading edge, and the red line represents the trailing edge. B) Mean differences between out-of-phase and in-phase contrast thresholds. Error bars indicate +/- 1 SEM.

3.3 Experiment 1C: The effect of smooth pursuit eye movements on the phase-dependent modulation of visual sensitivity in drifting stimuli

In this experiment, we investigated how smooth pursuit eye movements interact with the contextual effects on contrast sensitivity and phase-dependent modulation. This experiment aimed to examine the effects of relative phase between target and inducer (i), the target's position as leading or trailing relative to the inducer motion (ii), and the directional congruency between the gratings' drift direction and the pursuit direction (iii) on contrast sensitivity.

3.3.1 Methods

Ten observers participated in the experiment. Six of them were naïve to the purpose of the experiment. All observers had normal and corrected-to-normal vision. The stimulus configuration and properties were identical to those in Experiment 1A. However, the grating envelopes moved in parallel to the pursuit target in this

experiment. Thus, if the observers tracked the pursuit target accurately, then, the stimuli triggered the same retinal-image motion as in Experiment 1A. The pursuit target moved at a velocity of 10.45 º/s.

Observers were instructed to pursue the moving fixation dot with the smooth pursuit eye movements. In each trial, the pursuit target and the gratings started to move horizontally from a point at 10º eccentricity on the left or right side of the screen. The target and inducers appeared at the same time as in Experiment 1A and, after moving across the screen with the pursuit target, disappeared altogether. The task of the observers was to report whether the low contrast target grating appeared above or below the pursuit target. The stimulus duration was the same as in Experiment 1A (2100ms).

Figure 4 illustrates the condition that the target positioned at the trailing edge of inducer grating drifted in the direction opposite to pursuit. There were eight conditions which consisted of the combinations of the relative phase (in-phase vs. out-of-phase), the target position relative to the inducer motion (leading vs. trailing), and the directional congruency (whether the gratings drifted in the same or opposite direction to the pursuit). All conditions were tested in blocked trials except that the target position relative to the inducer motion, which was presented randomly in the same block.

In addition, there were two baseline conditions, where the target grating drifted in the same or opposite direction to the pursuit in the absence of an inducer. The baseline conditions were presented in the same experimental block. Observers completed nine blocks in random order. One experimental session (block) consisted of 280 trials that took approximately 20 minutes.

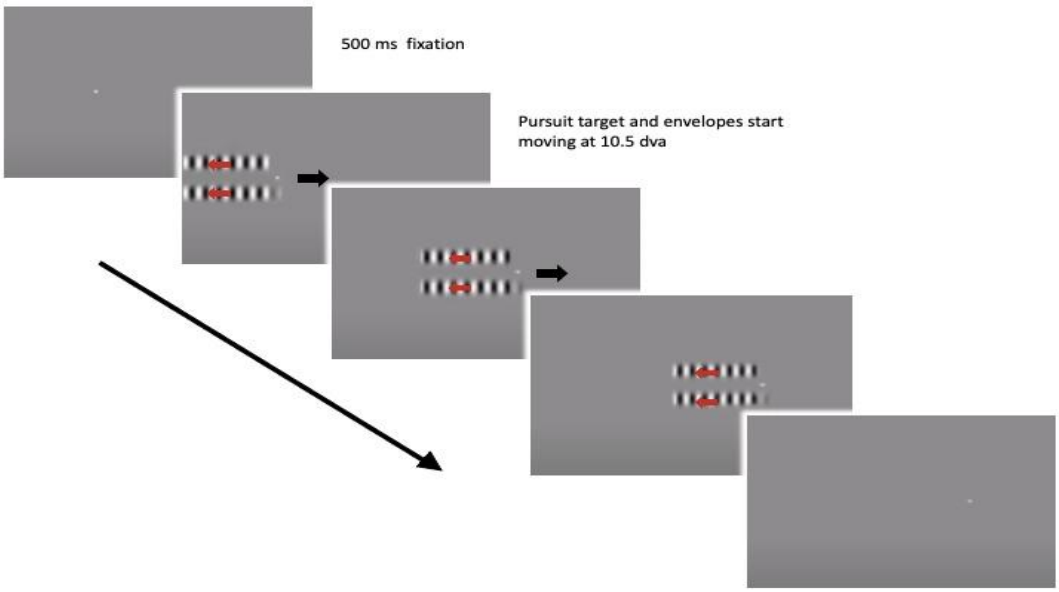


Figure 4. Outline of the Experiment 1C

The figure shows the condition, where the target positioned at the trailing edge is drifting in the direction opposite to the pursuit.

3.3.2 Results

A three-way repeated measures ANOVA was conducted to examine the effects of the relative phase (in-phase vs. out-of-phase), the directional congruency (same vs. opposite), and the target position (leading vs. trailing) on contrast thresholds. The analysis revealed significant main effects of relative phase ($F(1,9) = 34.37$, $p < .001$, $\eta_p^2 = .79$) and directional congruency ($F(1,9) = 45.12$, $p < .001$, $\eta_p^2 = .83$). Contrast thresholds for the target drifting in the same direction as the pursuit ($M = -1.42$ $SE = .16$) were lower than those that drifted in the opposite direction ($M = -0.81$ $SE = .17$). The main effect of the directional congruency was significant for all conditions, namely as the in-phase leading ($F(1,9) = 27.26$, $p = .001$, $\eta_p^2 = .75$), the in-phase trailing ($F(1,9) = 5.78$, $p = .04$, $\eta_p^2 = .39$), the out-of-phase trailing ($F(1,9) = 24.11$, $p = .001$, $\eta_p^2 = .73$) except for the out-of-phase condition, where the target was positioned at the leading edge ($F(1,9) = 1.02$, $p = .339$, $\eta_p^2 = .10$).

Moreover, the interaction between the target position and the relative phase was significant ($F(1,9) = 5.16$, $p = .049$, $\eta_p^2 = .37$). Although Bonferroni corrected pairwise comparisons were not significant, contrast thresholds for the in-phase targets were lower at the leading edge ($M = -1.51$ $SE = .19$) than at the trailing edge ($M = -1.41$ $SE = .19$). While this pattern was reversed for the out-of-phase targets, contrast thresholds were higher at the leading edge ($M = -.64$ $SE = .17$) than at the trailing edge ($M = -.90$ $SE = .18$) . Additionally, there was a marginally significant three-way interaction ($F(1,9) = 5.11$, $p = .05$, $\eta_p^2 = .36$).

Since we observed directional effects of pursuit and interactions, in further analyses, we compared the contrast thresholds in the pursuit conditions with the thresholds in the fixation obtained from Experiment 1A. All observers participated in both experiments, allowing us to test the effect of smooth pursuit in a within-subject design. Two separate 2x2x2 three-way repeated measures ANOVAs were run to see how smooth pursuit eye movements influenced the contrast thresholds compared to the fixation conditions for the same and opposite directions. Because this analysis aimed to observe the pursuit effect per se, only related results are reported (as the relative phase and the target position effects were reported in the earlier analyses). The first analysis showed that the contrast thresholds in the pursuit conditions in which the target drifted in the same direction as the pursuit were not statistically different from the fixation conditions (Figure 5), all *p*s > .05. On the other hand, when the target drifted in the direction opposite to pursuit, contrast thresholds were elevated compared to those in the fixation, indicated by the significant main effect of the pursuit ($F(1,9) = 34.21$, $p < .001$, $\eta_p^2 = .79$). The simple main effect analysis of the pursuit revealed that the decrease in the contrast sensitivity occurred in all target and relative phase conditions except for the out-of-phase target at the leading edge

(Figure 5). Overall, these results indicated that in the presence of an abutting inducer, smooth pursuit eye movements selectively decrease the contrast sensitivity for the stimuli moving (on the retina) in the direction opposite to the pursuit.

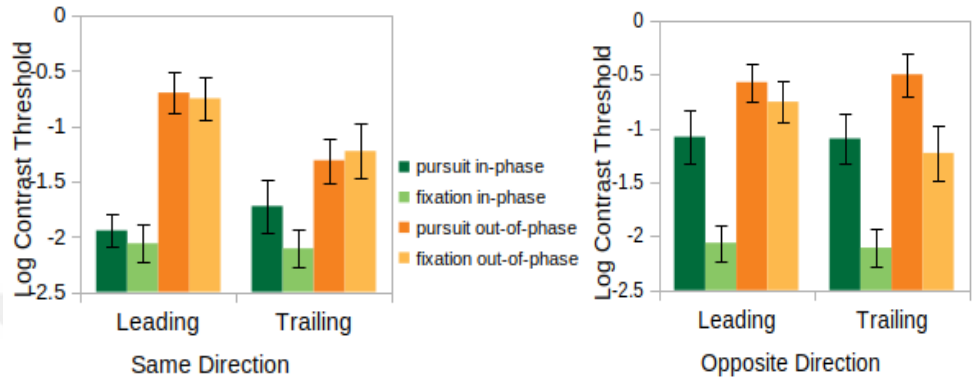


Figure 5. Mean contrast thresholds in Experiment 1C

The green bars represent the in-phase conditions, whereas the yellow bars represent the out-of-phase conditions. Darker bars represent the pursuit conditions, and the lighter bars represent the fixation conditions. Same direction refers to the conditions, where the gratings drifted in the same direction as the pursuit. Opposite direction refers to the conditions, where the gratings drifted in the direction opposite to the pursuit. Error bars indicate +/- 1 SEM.

Furthermore, we also investigated the directional effects on the phase-dependent modulation of contrast sensitivity by conducting a 2 (pursuit vs. fixation) x 2 (leading vs. trailing) repeated measures ANOVA on the difference between the out-of-phase and the in-phase thresholds. As shown in Figure 6, for the same direction, there were neither a significant main effect of smooth pursuit ($F(1,9) = 2.98$, $p = .119$, $\eta_p^2 = .25$) nor the interaction between the pursuit and target position ($F(1,9) = 1.63$, $p = .234$, $\eta_p^2 = .15$). On the other hand, a second ANOVA test for the opposite direction revealed a significant main effect of smooth pursuit, ($F(1,9) = 8.25$, $p = .018$, $\eta_p^2 = .48$) . There was also a significant interaction between the pursuit and target position ($F(1,9) = 7.38$, $p = .024$, $\eta_p^2 = .45$). This interaction

resulted from a significant simple main effect of pursuit on the difference between the out-of-phase and the in-phase thresholds at the leading edge ($F(1,9) = 13.10$, $p = .006$, $\eta_p^2 = .59$) and a non-significant simple effect of pursuit at the trailing edge ($F(1,9) = 1.98$, $p = .193$, $\eta_p^2 = .18$). Thus, when the target drifted in the direction opposite to the pursuit, smooth pursuit decreased the phase-dependent modulation of contrast sensitivity only at the leading edge of motion.

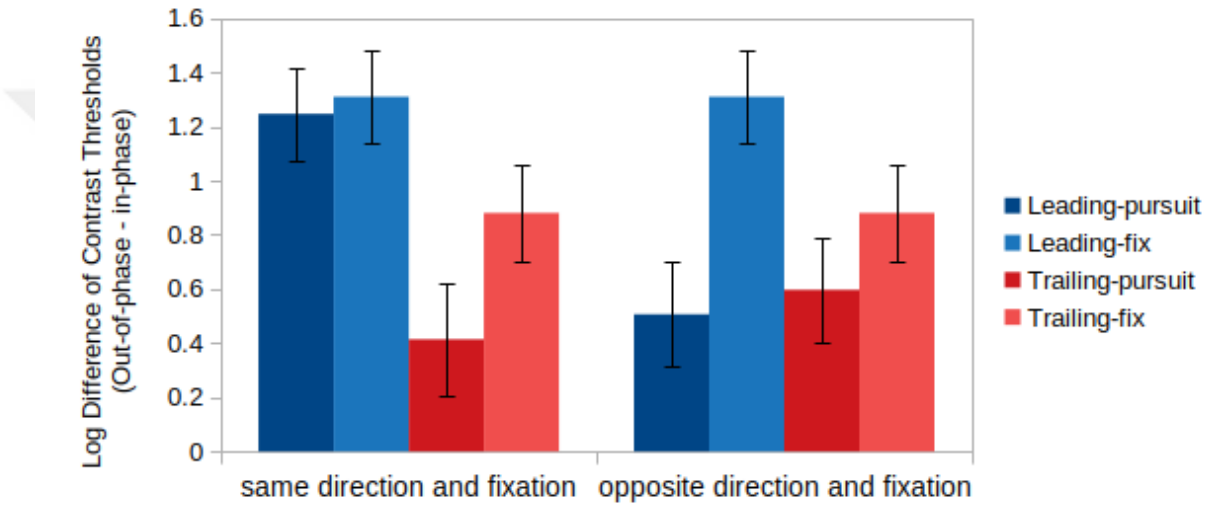


Figure 6. The comparison of the phase-dependent modulation between Experiment 1A and Experiment 1C

Mean differences between the out-of-phase and in-phase contrast thresholds across the target position conditions during pursuit (darker bars) and fixation (lighter bars). Blue bars represent the leading, and red bars represent the trailing conditions. Error bars indicate +/- 1 SEM.

To examine the effect of smooth pursuit eye movement and direction consistency on the targets without an inducer grating, a one-way repeated measures ANOVA was conducted on the contrast thresholds in the baseline conditions (i.e., two pursuit conditions followingly same and opposite directions, and the fixation condition). The results revealed a significant main effect, $F(2,18) = 7.17$, $p = .005$, $\eta_p^2 = .44$. Pairwise comparisons showed that the contrast thresholds were

significantly lower in the same direction (*M* = -2.30, *SE* = .32) than in the opposite direction (*M* = -1.58, *SE* = .70), *p*= .002. However, a difference was found neither between the fixation (*M* = -2.06, *SE* = .61) and the same direction (*M* = -2.30, *SE* = .32), *p*= .156, nor between the fixation (*M* = -2.06, *SE* = .61) and the opposite direction (*M* = -1.58, *SE* = .70), *p* = .077. As shown in Figure 6, smooth pursuit influenced the contrast sensitivity in a direction-specific manner. When the target drifted in the direction opposite to pursuit, contrast thresholds were elevated compared to those during the fixation. On the other hand, when the target drifted in the same direction as the pursuit, contrast thresholds slightly decreased, although this effect was only marginal and did not reach statistical significance. These results are in line with the previous studies showing a reduced contrast sensitivity for the motion opposite to pursuit which was attributed to feature-based attention (Schütz et al., 2009) and the directionally-selective suppression of magnocellular pathway (Tong et al., 2009).

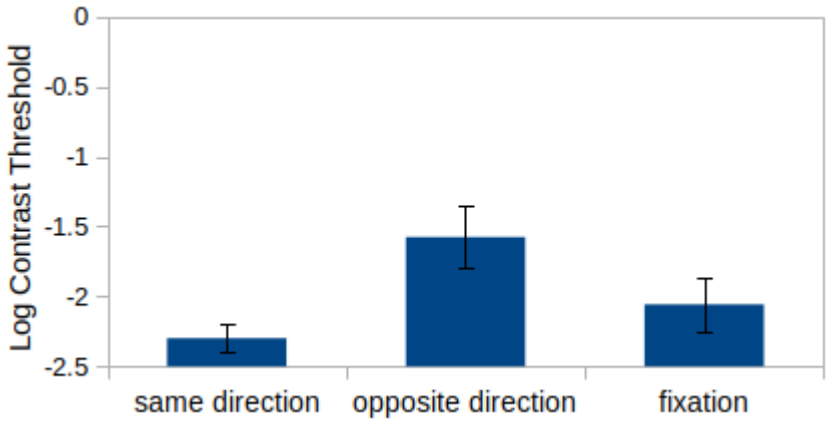


Figure 7. Mean contrast thresholds in the baseline conditions in Experiment 1C

Mean contrast thresholds of the baseline conditions to see the effect of smooth pursuit eye movement in the absence of high contrast inducer gratings. Error bars indicate +/- 1 SEM.

3.4 Experiment 1D: Phase-dependent modulation of visual sensitivity in static stimuli with moving envelope during smooth pursuit eye movements

In Experiment 1D, we investigated whether a retinal motion is necessary to induce phase-dependent modulation on contrast sensitivity in the presence of smooth pursuit eye movements. Additionally, this experiment also allowed us to observe how smooth pursuit eye movements interact with the reported surround modulation effects on static stimuli.

3.4.1 Methods

The stimuli configurations and features were identical to those in Experiment 1C with one exception that the sinusoidal gratings inside the moving envelopes were not dynamic. Therefore, during an ideal pursuit, no retinal motion was present. Target position was defined according to (1) the eye movement trajectory and (2) the leading and the trailing edges yielded by the inducer position. For instance, when the grating envelopes and the pursuit target moved from left to right and the inducer gratings abutted the target on the left hand side, this condition corresponded to the target positioned at the leading edge of the pursuit trajectory.

Experimental procedure was the same as that in Experiment 1C. In each trial, the target was either at the leading or at the trailing position (randomized across trials) relative to the pursuit direction. In-phase and out-phase conditions were blocked. In the baseline condition, the target grating without an abutting grating moved across the screen in parallel to the pursuit target. Observers completed three experimental blocks in randomized orders.

3.4.2 Results

We examined the effects of the relative phase and target position (relative to the pursuit trajectory) by conducting a 2x2 repeated measures ANOVA on the contrast thresholds. The analysis revealed a significant main effect neither for the relative phase ($F(1,9) = 3.69$, $p = .087$, $\eta_p^2 = .29$) nor for the target position ($F(1,9) = .03$, p = .873, np2 = .003, but a marginal interaction ($F(1,9) = 4.98$, $p = .053$, $\eta_p^2 = .36$). Moreover, the simple main effect of the relative phase was significant at the trailing edge ($F(1,9) = 7.65$, $p = .022$, $\eta_p^2 = .46$). To be more specific, the contrast thresholds for the in-phase target ($M = -.79$, $SD = .50$) was lower than those for the out-of-phase target ($M = -.38$, $SD = .47$) at the trailing edge of pursuit trajectory. Therefore, there was a phase-dependent modulation of contrast sensitivity at the trailing edge in favor of the in-phase targets. This result is surprising because whereas the effect of out-of-phase high contrast surrounds on the perceived contrast of static stimuli is generally facilitative (Yu, Klein & Levi, 2001), the effect of a high contrast in-phase surrounds are known to be suppressive (Ejima & Takahashi, 1985; Yu, Klein & Levi, 2001).

Additionally, as shown in Figure 7, thresholds were elevated irrespective of the relative phase when there was an abutting grating compared to the baseline condition ($M = -2.20$, $SD = .26$), indicating a phase-independent suppressive effect of the abutting grating.

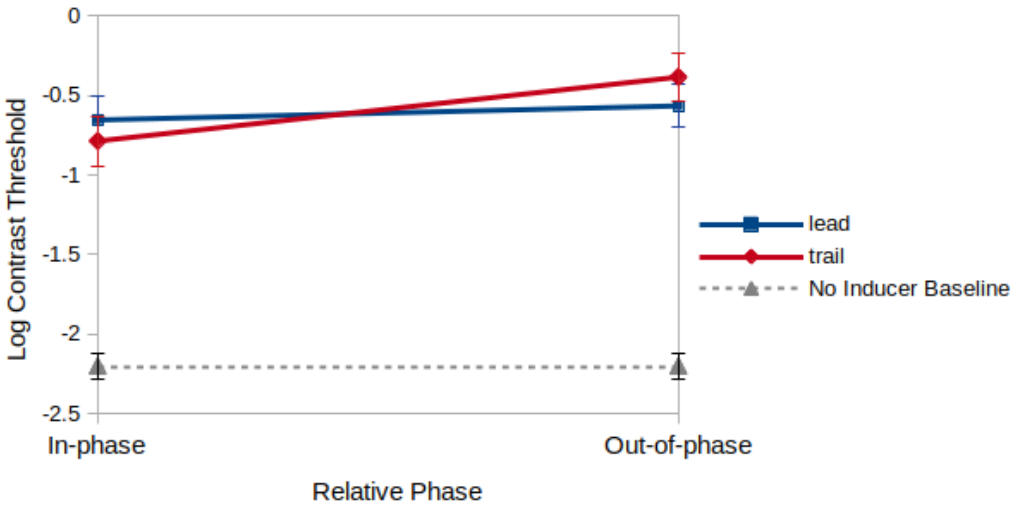


Figure 8. Overall results of Experiment 1D

Mean contrast thresholds at the leading edge (blue line) and at the trailing edge (red line) of the pursuit trajectory as a function of the relative phase. The dashed line represents the baseline condition. Error bars indicate +/- 1 SEM.

3.5 Experiment 2: Pursuit velocity

It has been shown that the luminance contrast sensitivity decreases with increasing pursuit velocity, which has been attributed to the increasing attentional demands as the pursuit velocity increases (Schütz, Braun, Kerzel, & Gegenfurtner, 2008). However, the results of Experiment 1C showed that there is no difference in the contrast thresholds between the pursuit and fixation conditions when the stimuli drifted in the same direction as the pursuit. Therefore, we concluded that the visual spatial attention has no remarkable effect on the contrast thresholds in our paradigm since our stimuli is presented nearer to the fovea. Following this, in Experiment 3, we investigate the effect of pursuit velocity on contrast sensitivity assuming independence from the effects of the spatial attention.

In order to explore the effect of sensorimotor gain induced by the smooth pursuit eye movements on contrast sensitivity and phase-dependent modulation, Experiment 1C was repeated with a lower pursuit velocity.

3.5.1 Methods

Six observers who participated in earlier experiments were also tested in Experiment 3. Three of them were naïve to the purpose of the experiment. Stimuli characteristics and the experimental procedure were the same as in Experiment 1C. The duration of the pursuit and the stimulus presentation was the same as earlier experiments, ~2100 ms. This time course with the slow velocity was achieved by changing the eccentricities of the onset and offset of the motion (pursuit) path. The pursuit velocity was 4.29º/s.

3.5.2 Results

To examine the velocity-dependency of the observed effects in Experiment 3, the contrast thresholds obtained from the low-velocity experiment were compared to those obtained with high-velocity pursuit (Experiment 1C).

We first investigated the effect of the pursuit velocity and the direction consistency on the targets without an inducer grating, using a 2x2 Repeated Measures ANOVA with two main factors, velocity (4.29 and 10.56º/s) and direction (same and opposite to pursuit). The analysis was conducted on contrast thresholds in the baseline conditions. This revealed a marginal main effect of velocity ($F(1,5) = 6.48$, $p = .052$, $\eta_p^2 = .57$). Moreover, there were a significant main effect of direction ($F(1,5) = 22.21$, $p = .005$, $\eta_p^2 = .82$) and the interaction between velocity and direction ($F(1,5) = 9.39$, $p = .028$, $\eta_p^2 = .65$). This interaction resulted from a significant simple effect of the velocity in the opposite direction ($F(1,5) = 8.78$, $p = .031$ $\eta_p^2 = .64$) and a non-significant effect in the same direction ($F(1,5) = .51$ $p = .508$, $\eta_p^2 = .09$). As shown in Figure 8, these results demonstrated that the contrast thresholds decreased with increasing pursuit velocity only for the targets drifting in

the direction opposite to the pursuit, implying that directionally selective effects of smooth pursuit are also velocity-dependent.

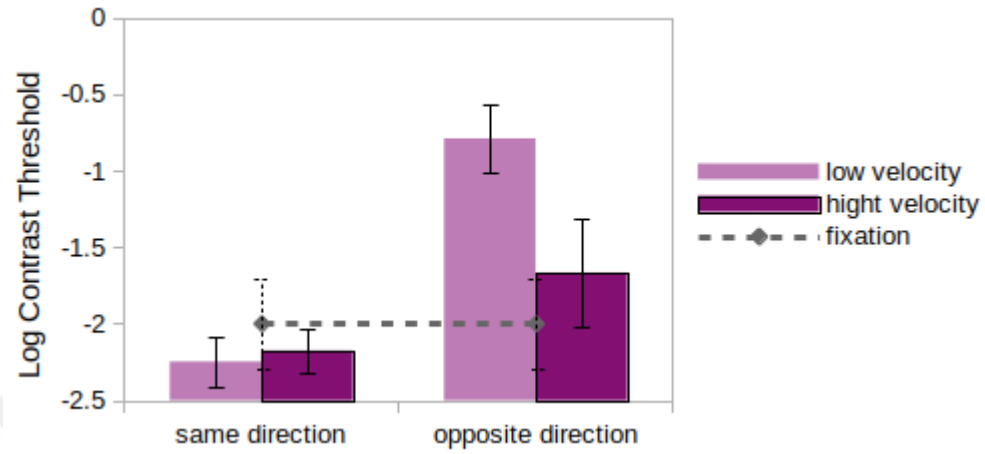


Figure 9. Mean contrast thresholds in the baseline conditions in Experiment 2

Mean contrast thresholds at high (10.56º/s) and low (4.29/s) pursuit velocity conditions. Dark purple bars represent high velocity, whereas lighter bars represent low velocity conditions. The dashed line represents the fixation condition. Error bars indicate +/- 1 SEM.

Two separate 2 (target position) x2 (pursuit velocity) x2 (relative phase) three-way repeated measures ANOVAs were run to see how pursuit velocity influences contrast thresholds in the presence of abutting inducers for the same and opposite directions. Only velocity-related results were reported. The first ANOVA was run for the same direction conditions and revealed a significant main effect of velocity ($F(1,5) = 8.48$, $p = .033$, $\eta_p^2 = .63$), indicating that the contrast thresholds increased with increasing pursuit velocity. There were also a significant interaction between velocity and target position ($F(1,5) = 11.11$, $p = .021$, $\eta_p^2 = .63$), and a three-way interaction ($F(1,5) = 11.95$, $p = .018$, $\eta_p^2 = .71$). This interaction resulted from the significant simple main effect of velocity for the in-phase target at the trailing edge ($F(1,5) = 9.18$, $p = .029$, $\eta_p^2 = .65$) and for the out-of-phase condition at the leading edge ($F(1,5) = 8.04$, $p = .036$, $\eta_p^2 = .62$). Overall results showed that the

contrast thresholds increased with increasing pursuit velocity, and that this pursuit velocity effect mainly occurred for the in-phase targets at the trailing and out-of-phase targets at the leading edge when the gratings drifted in the same direction as the pursuit.

The second ANOVA was conducted for the opposite direction conditions. The analysis revealed no significant main effect of velocity ($F(1,5) = 3.85$, $p = .107$, $\eta_p^2 = .44$) but a significant relative phase and velocity interaction ($F(1,5) = 11.57$, $p = .019$, $\eta_p^2 = .70$). The significant interaction resulted from the significant velocity effect in the in-phase condition ($F(1,5) = 7.60$, $p = .04$, $\eta_p^2 = .60$). The simple main effect analysis of the velocity also showed that the observed effect of velocity in the in-phase condition mainly occurred at the leading edge ($F(1,5) = 7.07$, $p = .045$, $\eta_p^2 = .59$). Thus, contrast thresholds in the in-phase conditions increased with increasing pursuit velocity, and this effect was stronger at the leading edge of motion.

Furthermore, we also investigated the effect of pursuit velocity on the phase-dependent modulation of contrast sensitivity by conducting a 2x2x2 repeated measures ANOVA on the difference between the out-of-phase and the in-phase thresholds with three factors, which are direction (same and opposite), velocity (4.29 and 10.56 º/s), and target position (leading and trailing). The results revealed a significant main effect of velocity ($F(1,5) = 7.88$, $p = .038$, $\eta_p^2 = .61$. The main effects were significant neither for the inducer ($F(1,5) = 3.83$, $p = .108$, $\eta_p^2 = .04$) nor for the direction ($F(1,5) = .02$, $p = .900$, $\eta_p^2 = .003$). The phase-dependent modulation of the contrast sensitivity was stronger at low pursuit velocity. Moreover, there was also a significant interaction between direction and velocity ($F(1,5) = 4.40$, $p = .09$, $\eta_p^2 = .47$) and three-way interaction ($F(1,5) = 4.48$, $p = .088$, $\eta_p^2 = .47$). Bonferroni-corrected pairwise comparisons revealed that the velocity effect was

significant for the opposite ($F(1,5) = 11.57$, $p = .019$, $\eta_p^2 = .70$) but not for the same direction ($F(1,5) = .23$, $p = .652$, $\eta_p^2 = .04$). Thus, for the opposite direction, the magnitude of phase modulation seemed to be regulated by pursuit velocity such that it decreased as the velocity increases. Additionally, the simple main effect analysis of velocity showed that this effect was mainly driven by the leading condition ($F(1,5) = 12.62$, $p = .016$, $\eta_p^2 = .72$). On the contrary, the same analysis also revealed that when the target was positioned at the leading edge and drifted in the same direction as the pursuit, the pursuit velocity influenced the phase-dependent modulation in a reversed fashion such that the magnitude of phase modulation at the leading edge increased with increasing pursuit velocity ($F(1,5) = 7.04$, $p = .045$, $\eta_p^2 = .59$).

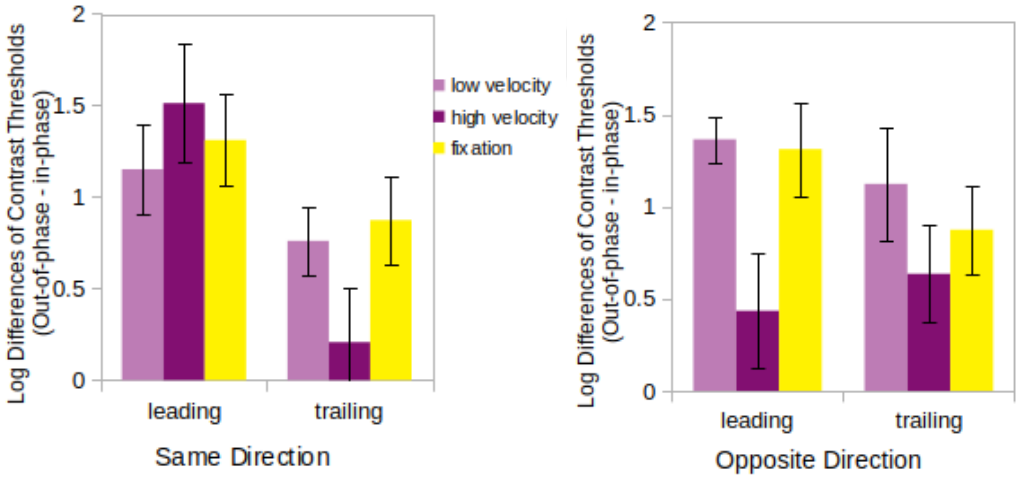


Figure 10. Mean differences between out-of-phase and in-phase contrast thresholds in Experiment 2

Purple bars represent pursuit conditions (i.e., light purple indicates low velocity, dark purple indicates high pursuit velocity). Fixation conditions were plotted for comparison. Error bars indicate +/- 1 SEM.

Overall, these results demonstrate that the pursuit velocity has a directionally selective effect on the contrast sensitivity in the absence of the abutting inducer. Contrast sensitivity increases with increasing pursuit velocity for the target drifting in

the direction opposite to the pursuit. On the other hand, in the presence of an inducer, contrast sensitivity decreases with increased pursuit velocity. This effect is generally present for the same direction but shows different phase-dependencies at the leading and trailing edges. In the opposite direction, velocity influences contrast sensitivity only in in-phase conditions and mainly at the leading edge.

Furthermore, the phase-dependent modulation is strongly dependent on pursuit velocity. In addition, the effect of velocity is also dependent upon the target position and directional congruency. When the target is positioned at the leading edge and drifts in the direction opposite to the pursuit, the phase modulation decreases as the velocity increases. On the contrary, when the target drifts in the same direction, this pattern is reversed, resulting in a reduced phase-dependent modulation with increasing pursuit velocity.

3.6 Experiment 3: Inducer Contrast

It is well known that the spatial summation is a highly contrast-dependent process, increases as the contrast decreases, and shows an in-phase facilitation effect for static stimuli at low contrast. Additionally, since motion blur is a more severe problem for high contrast stimuli, the difference of the phase modulation between the leading and the trailing edge must be reduced with decreasing inducer contrast if this effect is in fact modulated by motion deblurring.

3.6.1 Methods

Four observers including one naïve observer participated in the experiment. The experimental procedure and the stimuli were the same as in Experiment 1A, except that the inducer contrast was reduced to 50% Michelson contrast. However, our

preliminary data showed a ceiling effect with this inducer contrast even for the out-of-phase condition, in which the sensitivity is lower in general. Thus, in order to increase the thresholds and make a more accurate measurement, the target area was masked by a static transparent white noise.

3.6.2 Results

To examine the contrast-dependency of the phase-dependent modulation of the contrast sensitivity, we compared the thresholds obtained from this experiment to those obtained in Experiment 1A. All of the four observers participated in both experiments, thus, we tested the effect of inducer contrast in a within-subject design. A two-way repeated measures ANOVA was conducted to investigate the effects of inducer contrast (high vs. low contrast) and target position (leading vs. trailing) on the difference between the out-of-phase and the in-phase thresholds. This revealed a significant main effect of inducer contrast ($F(1,3) = 11.89$, $p = .041$, $\eta_p^2 = .80$). Whereas the simple main effect of the target position was not significant at low contrast ($F(1,3) = .11$, $p = .763$, $\eta_p^2 = .04$), it was found to be significant at high contrast condition ($F(1,3) = 44.11$, $p = .007$, $\eta_p^2 = .93$). These results, overall, showed that the difference in the phase-dependent modulation between the leading and the trailing edges reduced with a lower inducer contrast. However, as shown in Figure 10, this effect resulted from a reduced phase-dependent modulation at the leading rather than an increased modulation at the trailing edge. Therefore, the difference between the in-phase and out-of-phase thresholds depended on the contrast of the inducer grating mainly at the leading edge of motion.

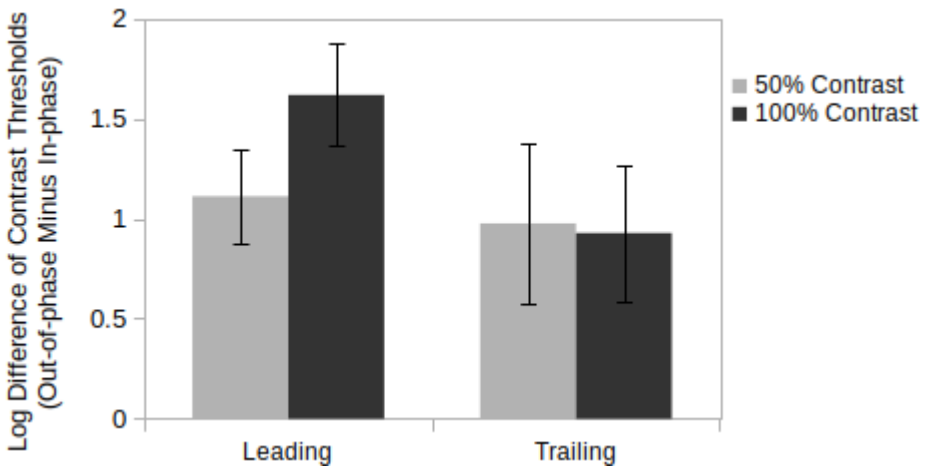


Figure 11. Mean differences between the out-of-phase and the in-phase contrast thresholds in Experiment 3

Dark gray bars represent the conditions with 100% Michelson contrast inducer gratings, and light gray bars represent the conditions with 50% Michelson contrast inducer gratings. Error bars indicate +/- 1 SEM.

CHAPTER 4

GENERAL DISCUSSION

Here, for the first time in literature, we investigated the effects of spatiotemporal context on the low-contrast stimuli in the presence of smooth pursuit eye movements. Our results provided evidence for the followings:

(1) The detectability of a drifting low-contrast sinusoidal target abutting a high contrast drifting grating is dependent on the relative phase of the sinusoidal waveforms of the two stimuli (Experiment 1A):
    a. When the sinusoidal waveforms of the two gratings are out of phase, the detectability of the low-contrast target is severely impaired.
    b. Moreover, this phase-dependent modulation of the contrast sensitivity is more evident at the leading edge than at the trailing edge of motion.

(2) The phase effect is absent for the second-order motion both at the leading and the trailing edges (Experiment 1B), indicating that the phase-dependent modulation is triggered only in the presence of spatio-temporal variations of luminance.

(3) The phase-dependent modulation of contrast sensitivity has a different dependency on the inducer contrast at the leading and trailing edges (Experiment 3). In particular, the phase-dependent modulation is more dependent upon the inducer contrast at the leading edge, increases with the inducer contrast, and invariant to changes in the inducer contrast at the trailing edge.

(4) Smooth pursuit influences the contrast sensitivity in a direction-selective manner. The contrast sensitivity for the gratings drifting in the direction

opposite to the pursuit is reduced compared to those drifting in the same direction as the pursuit (Experiment 1C).

(5) The effect of smooth pursuit on the phase-dependent modulation is also directionally selective and depends on the target position relative to inducer motion. The magnitude of the phase modulation reduces at the leading edge in the direction opposite to the pursuit (Experiment 1C).

(6) In the absence of an abutting grating, pursuit velocity alters the contrast sensitivity only for the gratings drifting in the opposite direction to the pursuit. To be more specific, the detectability of these targets is improved with increasing pursuit velocity (Experiment 1C, 2).

(7) The effect of the pursuit velocity on the phase-dependent modulation of contrast sensitivity is direction-selective and dependent on the target position (Experiment 1C, 2): The magnitude of the phase-modulation at the leading edge increases with the pursuit velocity when the gratings drifted in the same direction as the pursuit, a pattern which is reversed when they drifted in the opposite direction. The magnitude of the phase-dependent modulation at the trailing edge, however, is significantly influenced by neither the pursuit velocity nor the drift direction relative to the pursuit direction.

4.1 The phase-dependent modulation of contrast sensitivity during fixation

Findings from Experiment 1A showed that the detectability of targets is impaired when they abut an out-of-phase high-contrast inducer grating both at the leading and trailing edges of inducer motion, although this phase-dependent suppression is stronger at the leading edge. Moreover, the phase-dependent modulation of contrast sensitivity has a different dependency on inducer contrast at the leading and trailing

edges. In particular, Experiment 3 showed that the phase-dependent modulation is more dependent upon the inducer contrast at the leading edge, increases with inducer contrast, and invariant to changes in the inducer contrast at the trailing edge. Finding a suppression in the contrast sensitivity at the trailing edge in the presence of an out-of-phase abutting grating is consistent with the study of Arnold et al. (2014), where the authors linked the phase-dependent effects to a non-predictive spatial summation process and provided a contradictory evidence for the forward prediction model proposed by Roach et al. (2011). More specifically, Arnold et al. (2014) have attributed the reduction in the phase-dependent modulation of contrast sensitivity at the trailing edge to the inhibitory activity of motion deblurring. This conclusion was dependent on the observation that the contrast sensitivity is higher at the leading edge compared to the trailing edge in the in-phase condition (Arnold, Thompson, & Johnston, 2007; Roach, McGraw, & Johnston, 2011; Arnold, Marinovic, & Whitney, 2014). However, here, we found no significant difference in the contrast thresholds between the leading and trailing edges of motion in the in-phase condition. Within the context of Arnold et al.'s account, it is unlikely that an inhibitory process operating at the trailing edge modulates the phase sensitivity without reducing the contrast sensitivity. Moreover, any inhibition at the trailing edge would also elevate contrast thresholds above the baseline, which was not the case in our current data. Furthermore, in Experiment 3, should there be a suppression at the trailing edge, the inducers with lower contrast would decrease this inhibitory activity, and thus, lead to an increase in the phase-dependent modulation; yet our results did not support this hypothesis, either. Altogether, these findings suggest that the phase-dependent modulation of contrast sensitivity at the trailing edge is not a suppressed form of a process occurring at the leading edge, but rather relies on a separate neural

mechanism. In fact, consistent with this suggestion, Chambers (2016) demonstrated that the phase-dependent modulation at the leading and trailing edges have different spatial and temporal tuning properties. Although the underlying mechanism accomplishing the observed relative phase sensitivity is not clear yet, introducing a gap bigger than 0.5º between the target and the inducer diminished the observed phase-dependent effects in the previous studies (Roach, McGraw, & Johnston, 2011; Arnold, Marinovic, & Whitney, 2014), implying the involvement of early visual areas (V1), where the receptive fields of neurons are known to be small and phase sensitive (Hubel & Wiesel, 1968).

4.2 The effects of smooth pursuit eye movements on contrast sensitivity

When the target grating was presented without an abutting inducer grating, contrast thresholds were elevated for the targets drifting in the direction opposite to the pursuit compared to those drifting in the same direction. In addition, the sensitivities in the pursuit conditions were not significantly different from those in the fixation condition, except for a trend between the opposite direction and fixation conditions. Although the effect size was small, the increase in the contrast thresholds in the opposite direction conditions were observed for all subjects (N = 10) except one, and turned into a significant effect at low pursuit velocity as revealed by Experiment 2. Thus, the contrast sensitivity was selectively reduced for the motion opposite to the pursuit direction, which is in line with previous studies (Schütz et al., 2007; Tong et al., 2009). Schütz et al. and Tong et al. attributed this directional effect to different mechanisms, either to a feature-based attention (Schütz et al., 2007) or to a reduction in the gain of the magnocellular neurons for the opposite direction (Tong et al., 2009). Surprisingly, in Experiment 2, we showed that the observed impairment in the

contrast sensitivity becomes more evident at the low pursuit velocity (4.29º/s) than at the high pursuit velocity condition (10.56º/s), suggesting that the directionally selective impairment mechanism is modulated by a visual area informing about the eye velocity.

It has been shown that the neuronal responses in area MT are modulated by feature-based attention such that attending to a stimulus with non-preferred direction presented in the receptive field suppresses the response of relevant neurons (Martinez-Trujillo & Treue, 2004). Moreover, MT cells have also been shown to demonstrate suppression for motion opposite to the pursuit direction (Chukoskie & Movshon, 2009). Since the initiation and maintenance of pursuit require allocation of attention to the tracked objects, it is feasible to assert that neurons encoding the stimulus drifting in the direction opposite to the pursuit are suppressed due to feature-based attention to the pursuit direction (Schütz et al., 2007). However, this attentional account is not fully compatible with our observation of direction-specific pursuit velocity effect. It is unclear how the strength of feature-based attentional modulation attenuates at high pursuit velocities. Additionally, neurophysiological studies have shown that the activity of MT neurons depends on the speed on the retina, and that the speed tuning of these neurons does not change during pursuit (Inaba, Miura, & Kawano, 2011; Chukoskie & Movshon, 2009). In our experiment, the temporal frequency of the stimuli was 5 Hz corresponding to a speed of 5º/s on the retina for both pursuit velocity (high vs. low) and drift direction (same vs. opposite) conditions. Therefore, even if the directional suppression is regulated by the MT neurons, it would not be enough to explain the direction-specific pursuit velocity effects on its own. Thus, what we suggest is that a higher visual area modulates the strength of the suppression in different conditions. Chukoskie and

Movshon (2009) demonstrated that some cells in the area MST show suppression during pursuit in a non-preferred direction, and that they also change their speed tuning to compensate for the reafference motion induced by the pursuit. These findings indicate that these neurons encode the motion in the world-centered coordinates calibrating their responses according to the eye velocity. Since the pursuit speed and the retinal image speed were similar in the low velocity condition (i.e., 4.29º/s and 5º/s, respectively), one could argue that MST neurons could treat the motion of the grating drifting in the direction opposite to the pursuit as a reafferent motion and show greater suppression in that condition than in the high pursuit velocity condition (10.56º/s). However, previous studies (Schütz et al., 2007; Tong et al., 2009) showed that the contrast sensitivity is impaired at low temporal frequencies even when the pursuit speed is higher or lower than the target speed. Thus, a mismatch between the eye velocity and the retinal image velocity in the reafferent direction does not drive the contrast sensitivity. Another pursuit-related area is the frontal pursuit area (FPA) of the frontal eye fields (FEF) which have reciprocal connections with the areas MT and MST (Lynch & Tian, 2006). The FPA, the activation of which correlates with the pursuit velocity (Tanaka & Lisberger, 2001), is known to be responsible for the on-line gain control for smooth pursuit eye movements. The observed direction-specific effect of the pursuit velocity in our study, however, cannot be attributed solely to the FPA activity since we did not observe any change in the contrast sensitivity for the gratings drifting in the same direction as the pursuit. There is one possible suggestion that during pursuit, a feedback from a higher order area such as FPA may reduce the magnitude of the directional-selective suppression. Whatever the functional role or the underlying mechanism of the directional effect of pursuit velocity on contrast sensitivity, neural

areas informing about the eye velocity and gaze direction seem to play a regulatory role.

The direction of the pursuit velocity effect is also inconsistent with the findings showing a decrease in the luminance contrast sensitivity for low spatial frequencies with increasing pursuit velocity (Schütz, Braun, Kerzel, & Gegenfurtner, 2008). In Schütz et al. study, the authors attributed this effect to increasing attentional demands as the pursuit velocity increases. It is important to note that Schütz et al. (2008) used a briefly flashed line carrying no net motion in order to avoid any retinal slip. Using translational motion, however, what we observed here was the reverse of this pattern. Thus, the methodological differences in the stimulus duration and the drift condition between the two studies might account for the discrepancies in the findings. In this thesis, we showed, for the first time that the pursuit velocity effects are directionally selective, occurring only for the motion opposite to the pursuit direction.

During saccades, the visual sensitivity for low spatial frequency luminance stimuli is impaired, and the temporal impulse response function (TIRF) speeds up (Burr & Morrone, 1996). Burr and Morrone (1996) have attributed the speeding up of the TIRF to a decrease in the gain of magnocellular neurons at low temporal frequencies (Benardete, Kaplan, & Knight, 1992). Similarly, Tong et al. (2009) demonstrated that the contrast sensitivity for the motion opposite to the pursuit direction decreases at low temporal frequencies (i.e., 4-6 Hz), and the TIRF speeds up. Additionally, Schütz et al. (2007) observed a nonsignificant trend for a shift of the temporal contrast sensitivity function to higher temporal frequencies for the gratings drifting in the opposite direction. Together with these findings, Tong et al. argued that increasing the visual processing speed for the direction opposite to

pursuit helps to reduce motion blur induced by the eye movements since a stationary background moves in the direction opposite to pursuit on the retina. Consistent with this argument, it has been reported that the critical chromatic flicker frequency is higher during pursuit than during steady fixation but only when the retinal motion is produced by the eye movements, implying an improvement in the temporal resolution for color in the reafferent motion trajectory (Terao, Watanabe, Yagi, & Nishida, 2010). This direction-selective effect is inconsistent with the account of Schütz et al. (2008; 2009), who suggested a rather general increase in the contrast gain in the parvocellular pathway during the pursuit eye movements. Terao et al. (2010), however, used a dark background to include the luminance motion mechanism, hence this methodological difference might account for the conflicting findings as they also suggested so in their report. They also argued that since the visual stimulus in Schütz et al. (2008) was a stationary horizontal line flash on a background, the reported improvement in the isoluminant chromatic sensitivity during the pursuit could be related to the observed perceptual enhancements for the stimuli which are environmentally stationary but moving on the retina in the direction of the reafferent motion.

In a recent study conducted in our laboratory, we demonstrated that the pursuit enhances the color contrast sensitivity for isoluminant gratings regardless of the drift direction of the target relative to the pursuit trajectory, supporting the account of Schütz et al. on the general enhancement in the contrast gain in the parvocellular pathway during pursuit (Tanrıverdi, Alashan, Ekinci, & Ayhan, 2021). Moreover, adding luminance contrast to the chromatic gratings gradually reduced the sensitivity for the direction opposite to the pursuit without affecting the detectability of the gratings drifting in the same direction. These results point out that the

direction-specific reduction in the sensitivity for the opposite direction is mediated by a luminance-based mechanism and gradually decreases with decreasing luminance contrast in the chromatic stimuli and disappears at isoluminance. In a further experiment, we also demonstrated that the contrast thresholds are lower for isoluminant gratings drifting in the direction opposite to the pursuit compared to those drifting in the same direction, although this is an effect of a small magnitude with no statistical significance. Note that because the stimuli were of lower speed in our chromatic paradigm, they remained for a longer time on the screen per trial (i.e. 2600ms); we think that a shorter presentation duration in the achromatic paradigm might have increased the difference in the contrast thresholds between the two direction conditions.

That the reduction in the luminance contrast sensitivity for the motion in the opposite direction is tuned to lower temporal frequencies (Tong et al., 2009) and the color and high spatial frequency luminance sensitivities are enhanced during smooth pursuit eye movements (Schütz et al., 2008) suggest that the parvocellular boosting is accompanied by a directionally selective decrease in the gain of the magnocellular pathway, agreeing with Tong et al. (2009). Such a mechanism would contribute to reducing motion blur and maintaining perceptual stability during pursuit. It has been shown that the pursuit-related enhancement for the parvo-related stimuli begins before the pursuit initiation, implying a top-down modulation from a visuomotor area responsive to extraretinal signals (Schütz et. al., 2008). We argue that a similar feedback modulation might also mediate the visual processing in the magnocellular pathway in a direction-selective manner. Considering the changes in the neuronal response and the speed tuning with respect to pursuit direction and pursuit velocity (Chukoskie & Movshon, 2009) and its connections to FPA, the area MST stands to

be a possible candidate to mediate a directional selective and velocity-dependent modulation.

4.3 The interaction between smooth pursuit and phase-dependent modulation of contrast sensitivity

Experiments 1C and 2 revealed that the phase-dependent modulation has a different dependency on the pursuit velocity at the leading and trailing edges. Moreover, the effect of pursuit velocity at the leading edge depends on whether the gratings drift in the direction opposite to or same as the pursuit. In particular, as revealed by Experiment 1C, the difference between the in-phase and out-of-phase contrast thresholds for the targets drifting in the direction opposite to pursuit is reduced compared to that in the fixation condition (Experiment 1A). This effect is prominent at the leading edge and results from an increment in the contrast thresholds for the in-phase condition. In contrast to the interaction between the directional congruency and the relative phase at the leading edge, contrast thresholds are elevated at the trailing edge regardless of the relative phase between the target and inducer. On the other hand, when the gratings drift in the same direction as the pursuit, contrast thresholds, as well as the difference between the in-phase and anti-phase thresholds at both the leading and trailing edge are similar to those during steady fixation, indicating that the smooth pursuit has no significant effect on the contrast sensitivity and the phase-dependent modulation in the same direction at high pursuit velocity (i.e., 10.56 deg/sec). During pursuit, the phase-specific effects are dependent on the interaction between whether the gratings drifted in the direction opposite to or the same as pursuit and the pursuit velocity, and show different patterns for the leading and trailing edges of motion. Specifically, at the trailing edge, the phase-dependent

modulation of contrast sensitivity decreases as the pursuit velocity increases, regardless of whether the gratings drifted in the direction opposite to or the same as the pursuit. However, this is only a trend with a nonsignificance and is not stronger than the effects on the leading edge. The sign of the change in the phase-dependent modulation at the leading edge differs with respect to whether the gratings drifted in the direction opposite to or the same as pursuit. When the gratings drift in the same direction as the pursuit, the difference between the in-phase and out-of-phase thresholds increases with increasing pursuit velocity. This effect results from an elevation in the thresholds for the out-phase condition at high velocity, suggesting that forward retinal motion which is also congruent with the eye movement trajectory suppresses the visibility of an incongruent stimulus along the retinal motion trajectory as the pursuit velocity increases.

Roach et al. (2011) asserted that facilitating the sensory signals which are congruent with the forward predictions based on a prior pattern may contribute to the mechanisms which improve the sensitivity in the predictable trajectories (Grzywacz, Watamaniuk, & McKee, 1995) by reducing the suppressive effects of the surround context. Sensory signals which are incongruent to internal predictions, on the other hand, weaken this facilitation when the inducer and target are out-of-phase. Even when we presume that a separate process takes place at the trailing edge, a prediction based on the spatial pattern of the prior motion is not plausible to explain the modulation at the leading edge as shown by Chambers (2016). However, smooth pursuit eye movements might interact with a non-predictive process underlying the phase-dependent modulation. It has been shown that predicting the trajectory of a moving object is better when the object is smoothly tracked compared to the steady eye condition even when the retinal movement is comparable under both conditions

(Spering, Schütz, Braun, & Gegenfurtner, 2011). In addition, it is also known that the smooth pursuit response becomes more subject to perturbations in the pursuit target speed as the eye movement velocity increases (Schwartz & Lisberger, 1994). We suggest that when an out-of-phase low contrast stimulus is located ahead of a forward retinal motion in the same direction as the pursuit, the spatiotemporal discontinuity might lead to a poorer motor tracking performance as the pursuit velocity increases. Thus, suppressing the visibility of such incongruent target may benefit the pursuit maintenance and motion prediction. When the target is positioned at the trailing edge during pursuit, however, since the high contrast abutting inducer grating is ahead of the pursuit target, where the attention is to be allocated (Chen, Valsecchi, & Gegenfurtner, 2017), a disruption in the spatiotemporal continuity in this case would have less influence on the maintenance of the pursuit and the extrapolation of the motion trajectory since the high contrast inducer may already drive the pursuit well.

Although the spatiotemporal continuity is not sufficient to induce a phase-dependent effect on contrast sensitivity as shown by Arnold et al. (2014) and Chambers (2016), one may assume that the degree of the suppression in the out-of-phase conditions might be driven by such function in the presence of smooth pursuit eye movements.

Considering that tracking the moving objects enhances motion prediction compared to the condition where the eyes are steady (Spering, Schütz, Braun, & Gegenfurtner, 2011), our results imply a prediction-based mechanism in the visuomotor processing during pursuit, which may also be mediated by the pursuit velocity and modulate the phase-dependent modulation of contrast sensitivity. Suppressing signals that disrupt the spatiotemporal continuity, which might

otherwise lead to perturbations, along the eye movement trajectory would contribute to maintaining pursuit accuracy at higher pursuit velocities. The reduction in the phase-dependent modulation in the opposite direction and at the trailing edge also supports this suggestion since the mechanism underlying the phase-dependent modulation could not benefit from a predictive strategy induced by smooth pursuit eye movements when the retinal motion is in the reafferent motion trajectory. Moreover, the reduced gain in the magnocellular pathway in the reafferent direction may also cause a suppression in the cortical process underlying the phase-dependent effect.

4.4 Conclusions

We provide evidence that the reduced phase-dependent modulation at the trailing edge does not result from an inhibitory motion deblurring process. Although the underlying mechanism accomplishing the phase-dependent modulation is not yet clear, our results suggest that different processes take place at the leading and trailing edges since the effect is stronger and more dependent upon the inducer contrast at the leading edge of motion.

Moreover, smooth pursuit eye movements interact with the phase-dependent modulation of contrast sensitivity, especially at the leading edge of retinal motion. Specifically, while the phase modulation decreases with pursuit velocity in the reafferent motion direction, it increases with pursuit velocity when the direction of the retinal motion and the pursuit trajectory are the same. These direction-specific and pursuit velocity-dependent effects that occur at the leading edge are broadly in line with the findings on enhancing motion prediction and differential visual processing in the reafferent direction during pursuit.

APPENDIX A

ETHICS COMMITTEE APPROVAL



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

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"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].

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

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