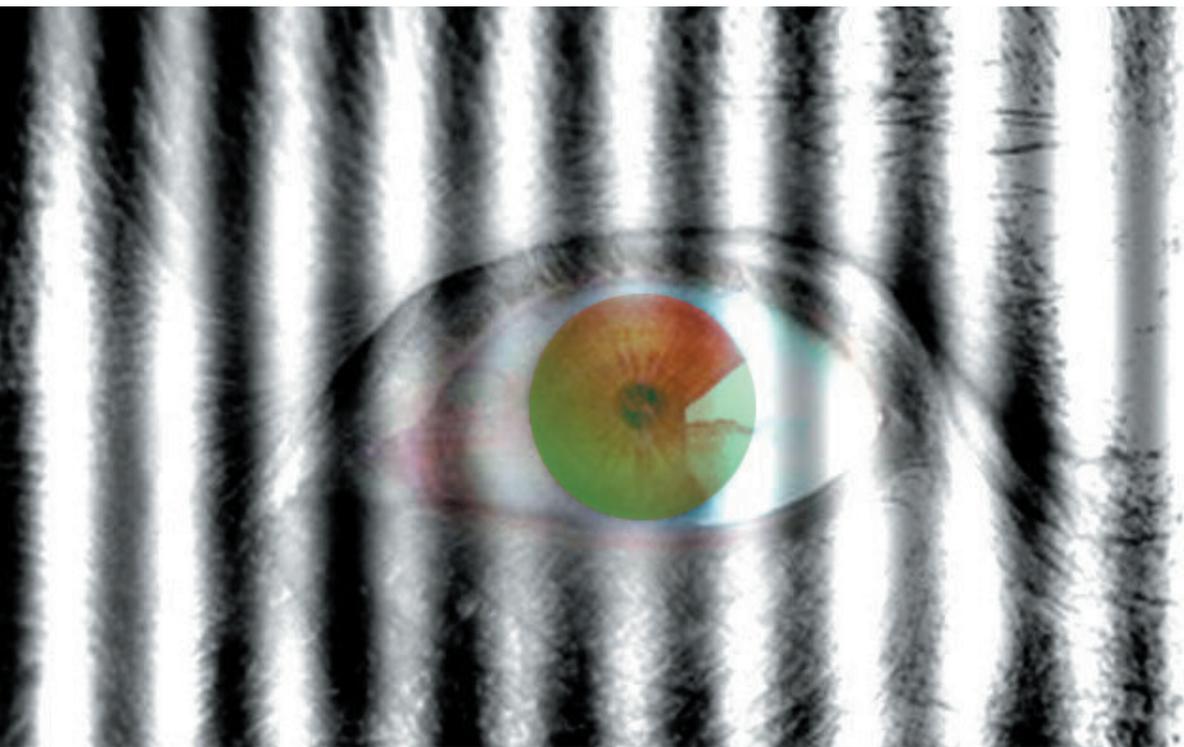


Binocular rivalry in context



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Binoculaire rivaliteit in context

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voor mijn vader en moeder

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Chapter 1

Introduction

Visual perception of an object is often affected by the visual context by which the object is surrounded. Take for example the stimuli presented in Figure 1. In Figure 1a, the perceived luminance of the ring is different depending on the background against which it is presented, although the luminance of the two rings is physically the same in both cases. Also, finding the object with an orientation different from the other objects in Figure 1b is easier when the difference in orientation between the target object and the context is larger. In the first example, the appearance of a local stimulus is influenced by the background. In the second example, the context determines how much a local stimulus stands out from the background. In both examples, the visual context in which the stimulus is embedded affects some aspect of visual perception of the stimulus.

Much knowledge about how visual context affects visual processing comes from neurophysiological studies in non-human species. Neurons engaged in visual processing often respond optimally to a stimulus feature presented to a certain part of the visual field. Presenting stimuli *outside* this so-called classical receptive field often influences the response to an optimal stimulus presented *within* the classical receptive field. Such neurons show a center-surround organization; presenting stimuli to the surround of the receptive field modulates the response to the center. These neurons provide a possible circuitry for contextual modulations observed at the perceptual level. However, knowledge about the perceptual outcome of such neural organization is scarce. In addition, it is generally not possible to study visual processing at the level of individual neurons in humans. Therefore, the present dissertation discusses contextual modulation of visual processing using a psychophysical approach. The central question in this dissertation is: how does visual context modulate visual perception? The last chapter deals with a slightly different (but related) question: what is the contribution of visual attention to contextual modulation of visual perception? Visual attention often needs to be distributed over several objects (for example while driving a car). In the last chapter it is investigated how visual perception of an object is affected by the amount of attention taken up by the processing of contextual stimuli.

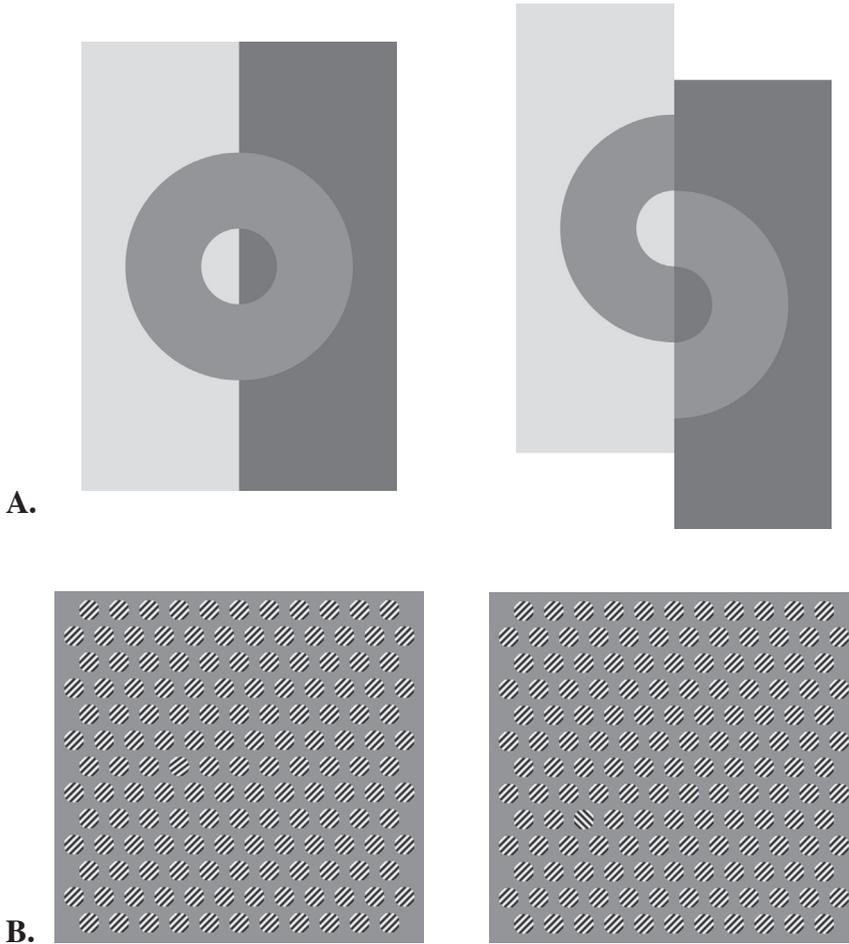


Figure 1. Contextual influences on visual perception. **A.** The Koffka ring. If the ring is cut in two, the context in which the two halves are embedded makes them appear to have different luminances. **B.** If the difference in orientation between target object and the other objects is small, the target is difficult to find.

Throughout this dissertation, hypotheses on how visual context affects visual perception are often based on neurophysiological findings. The reason for this is straightforward: visual perception is presumably *the result* of neural processing. In the experiments described, binocular rivalry serves as a tool to study contextual modulation at the perceptual level. Before introducing binocular rivalry and arguing why it is useful to study contextual modulation in vision, studies on contextual modulation of visual processing are discussed.

Contextual modulation at the neural level

One of the major scientific breakthroughs of the 20th century was the finding that neurons in the primate brain often respond to specific stimulus features. The hallmark findings of Hubel and Wiesel (1968) established that neurons in the visual cortex respond to specific visual features, presented at a specific location of the visual field. For example, a specific neuron might respond to a stimulus with a horizontal orientation, presented at the left upper part of the visual field. Presenting the stimulus elsewhere in the visual field will not activate the neuron beyond a baseline level, nor will it respond to a stimulus that has a different orientation. The concept of a neuron responding to a specific area of the visual field has been labeled the classical receptive field (Hartline & Graham, 1932).

Stimulus-selective responses have also been described for characteristics such as color (or chromaticity) and motion (see Livingstone & Hubel, 1988). For example, monkey middle temporal cortical area (MT) contains neurons that are tuned for the direction as well as the speed of visual motion (Mikami, Newsome & Wurtz, 1986). However, the response of a neuron has been shown to be dependent on visual stimulation in proximity of its classical receptive field (Blakemore & Tobin, 1972). For example, presenting the same feature in proximity of the classical receptive field of a neuron can modulate its response. This contextual modulation has been observed for multiple sensory modalities like visual processing (Blakemore & Tobin, 1972), auditory processing (Knudsen & Konishi, 1978), and olfactory processing (Yokoi, Mori & Nakanishi, 1995). In visual processing, contextual modulation is observed at a multitude of visual processing stages. For example, contextual modulation of neuronal responses has been observed at the level of the retina (Barlow, 1953), the lateral geniculate nucleus (LGN; McIlwain, 1964), the primary visual cortex (V1; Blakemore & Tobin, 1972), middle temporal area (MT; Allman, Miezin & McGuinness, 1985) and middle superior temporal area (MST; Eifuku & Wurtz, 1998).

In vision, contextual modulation of neural responses has been studied extensively in the domain of visual motion processing. For example, Allman et al. (1985) showed that the response of MT-neurons to their preferred direction of motion could be inhibited by presenting the same direction of motion to their non-classical surround. Most neurons were inhibited by surround motion; the response to center motion decreased when surround motion was presented. However, facilitation of responses was also observed; in that case surround motion increased the response to motion presented to the center. Whether surround interactions inhibited or facilitated the response to the center depended largely on the difference in motion directions between center and surround. Inhibition was mostly observed when center and surround moved in the same direction; facilitation was more prominent when center and surround contained motion in different directions. Later studies both replicated and extended the results of Allman et al. (e.g. Born & Tootell, 1992; Bradley & Andersen, 1996; Raiguel,

van Hulle, Xiao, Marcar & Orban, 1995; Tanaka, Hikosaka, Saito, Yukie, Fukada & Iwai, 1986).

Several studies have attempted to provide a functional framework for surround interactions in visual processing neurons. For example, it has been argued that these interactions are important for segregating figure from ground (Gautama & van Hulle, 2001) and in the construction of three-dimensional shape from motion (Koenderink & van Doorn, 1992). The behavioral relevance of surround interactions is also highlighted by recent studies showing contrast-dependency of surround interactions. For example, Pack, Hunter and Born (2005) showed that the nature of surround interactions of MT-neurons of the macaque was dependent on the contrast at which the stimuli were presented. When center and surround moved in the same direction at high luminance contrast, the response to the center was inhibited, whereas this response was facilitated when contrast was low. It has been argued that such adaptive surround interactions provide a means to effectively code visual motion under a variety of visibility conditions (Tadin, Lappin, Gilroy & Blake, 2003). When visibility is poor (contrast is low), it makes sense to boost the response to the center, when visibility is good (contrast is high), the response can be reduced.

Contextual modulation at the perceptual level

At the level of perception, contextual modulation of visual processing has been observed for many stimulus characteristics (see Albright & Stoner, 2002). In motion perception for example, it has been found that surround motion can influence perception of ambiguous center motion. Motion contrast refers to the finding that a motion surround makes ambiguous center motion appear to move in the direction opposite to the surround motion (see Reinhardt-Rutland, 1998). Also, a surround can make ambiguous center motion appear to move in the same direction (motion capture; Ramachandran, 1987). Murakami and Shimojo (1996) attempted to disentangle the conditions in which either motion contrast or motion capture were present (which they labeled contrast- and assimilation-type motion induction respectively). They found that the size of a motion stimulus and the eccentricity at which the stimulus was presented was crucial in determining whether contrast- or assimilation-type surround induction would occur. With increasing eccentricity, assimilation-type induction was observed for small stimuli, whereas contrast-type induction was observed for larger stimuli. The authors posed that center-surround interactions in visual motion processing neurons (of the kind described above) were responsible for the inductive effect of surround motion.

The same conclusion was reached by Tadin et al. (2003). In their study, observers judged the direction of motion of a motion stimulus with varying size. The time it took observers to discriminate between leftward and rightward motion increased with increasing size of the motion stimulus. However, if the motion stimulus was presented at low contrast, the

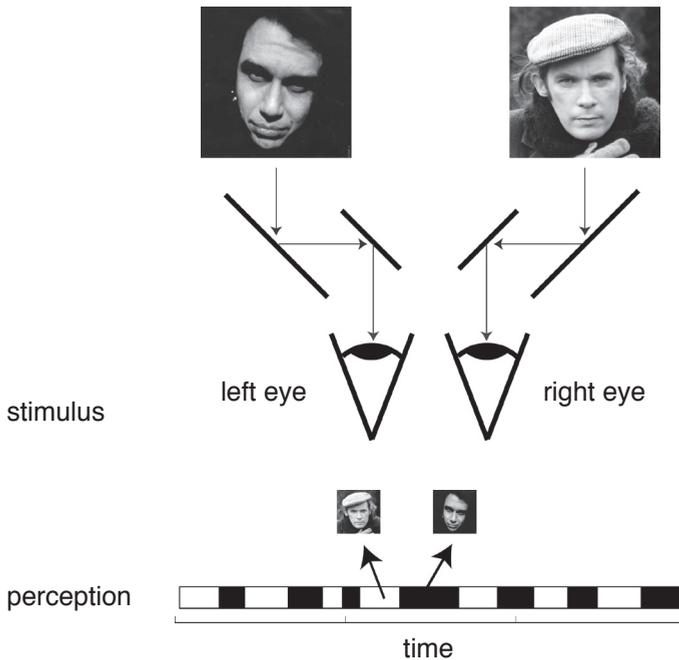


Figure 2. Simplified representation of a stimulus presentation leading to binocular rivalry. When each eye is presented with a different stimulus via a mirror-stereoscope, the dominant percept alternates in time.

time to discriminate between both directions of motion decreased with increasing size. In an additional experiment, the motion aftereffect (MAE, see Anstis, Verstraten & Mather, 1998) was measured using an adaptation stimulus of varying size. The test stimulus always had the same size, which was slightly smaller than the smallest adaptation stimulus used. At high contrast, the MAE decreased with increasing size of the adaptation stimulus. At low contrast, however, the MAE increased with increasing size of the adaptation stimulus. The authors claimed these results to be perceptual correlates of center-surround interactions at the neural level. Furthermore, their results are in line with those of Pack et al. (2005): large, high-contrast motion stimuli are presumably subject to surround inhibition, degrading the signal representing the motion. In contrast, large, low-contrast stimuli are presumably subject to surround facilitation, improving the signal representing the motion.

Binocular rivalry

In the studies presented in this dissertation, binocular rivalry is used as a tool to study contextual modulation in visual perception. Binocular rivalry has intrigued scientists from the

beginning of modern psychology at the end of the 19th century. When each eye is presented with a different stimulus (also called target), perception alternates between the two images (Figure 2). That is, for a few moments the stimulus presented to the left eye will be perceived (the left eye stimulus is perceptually dominant), after which dominant perception switches to the stimulus presented to the right eye (the left eye stimulus is suppressed). This process of dominance and suppression of the rival stimuli will continue for as long they are presented.

Throughout its scientific history it has been debated whether binocular rivalry reflects visual competition at a low stage of visual processing, or whether processing stages higher up the visual processing hierarchy are involved (Hering, 1964; Helmholtz, 1962; Blake, 1989; Logothetis, 1998). From Levelt's (1965) seminal monograph, the low-level view of binocular rivalry became popular. In a number of propositions, Levelt described binocular rivalry dynamics using low-level stimulus characteristics like luminance contrast. Levelt's first proposition states that the predominance of a stimulus will increase when its stimulus strength is increased. For example, increasing the contrast of one target will increase its predominance. Levelt's second proposition describes the relation between stimulus strength and perceptual dominance of each target. According to this proposition, changing stimulus strength of one rival target will affect dominance of the other target. For example, when the contrast of one target is lowered, the time this target is dominant will be unaffected. However, the dominance of the other target will increase. Likewise, increasing the contrast of one target will decrease the dominance of the other target. Lastly, the third and fourth propositions state that increasing the stimulus strength (whether of one target, or of both) will increase the alternation rate. Since the response of neurons at early stages of processing (i.e. V1) is closely related to stimulus contrast (Sclar & Freeman, 1982), these properties of binocular rivalry are believed to reflect a low-level site of processing to give rise to binocular rivalry.

More recently, Blake (1989) also supported the view that binocular rivalry reflects low-level processing characteristics. Blake formalized several findings on binocular rivalry and proposed a theory of binocular rivalry. In this view, binocular rivalry is the result of monocular competition at early levels of processing (i.e. V1). This has been taken to imply that binocular rivalry is largely dependent on which eye receives which stimulus: that is, that the dominant percept will alternate between the left- and the right-eye view.

Throughout the scientific history of binocular rivalry, the low-level view has been challenged by the high-level view. For example, Helmholtz (1962) claimed that it was possible to control rivalry by attention. Although attentional control over rivalry is still subject to debate (see chapter 6), the high-level view has been supported by findings that are difficult to reconcile with a low-level view of binocular rivalry. For example, Diaz-Caneja (1928) divided two dissimilar images (a concentric and a horizontally oriented grating) in two halves. The left half of one image was connected to the right half of the other image, and vice versa. When these images were presented dichoptically, observers also perceived the concentric or

oriented grating as a whole. This result cannot be explained by eye-based rivalry. However, as shown by Blake, O'Shea and Mueller (1992), rivalry is a local process; when the size of rival stimuli increases, the dominant percept can contain parts of both rival stimuli. Thus, with large targets, one part of the dominant stimulus may contain the left eye's view, while another part originates from the right eye. This does not preclude the possibility that rivalry is based on monocular competition; it *does* however mean that rivalry cannot be solely eye-based.

More recently, Logothetis (1998) has advocated the high-level view. In one study, Logothetis, Leopold and Scheinberg (1996) used a clever method showing that binocular rivalry can occur at the stimulus-representation level. In their study they quickly alternated the targets between both eyes. Interestingly, the time-course of perceptual alternations was much slower than predicted by eye-based rivalry. In fact, the alternation rate resembled that of 'classical' rivalry during which each image is presented to one eye only. Although Lee and Blake (1999) showed that this type of rivalry only occurs under limited conditions, this finding has been taken as strong support for the high-level view.

As is true for many perceptual phenomena, binocular rivalry has recently been investigated using functional Magnetic Resonance Imaging (fMRI). Using this technique, both the low-level and high-level view has gained new support. Lumer, Friston and Rees (1998) and Tong, Nakayama, Vaughan and Kanwisher (1998) reported that several anatomical regions outside the visual cortex were active during binocular rivalry. For example, Tong et al. (1998) correlated dominant perception of a house and a face to the Parahippocampal Place Area (PPA) and the Fusiform Face Area (FFA) respectively. However, these findings do not exclude the possibility that dominance-related activity was inherited from visual processing at earlier stages. Polonsky, Blake, Braun and Heeger (2000) and Tong and Engel (2001) both showed that dominant perception of rival stimuli was correlated with V1 activity. Tong and Engel studied fMRI activity in monocular areas in V1 corresponding to the blind spot. This area is greatly activated by stimulation of the ipsilateral eye. Their experiments showed that this area was active when a target presented to the ipsilateral eye was perceptually dominant. When a target presented to the blind spot eye was perceptually dominant, activity was suppressed. Their study has been taken as evidence that binocular rivalry is the result of competition at the level of V1.

Although the findings described above have been interpreted in favor of either the low-level or the high-level view, several authors have recently argued that a distributed network of visual processing areas is involved in binocular rivalry (e.g. Nguyen, Freeman & Alais, 2001; Logothetis & Blake, 2002). Also, effort has been made to incorporate diverse findings on binocular rivalry into a single theory. Wilson (2003) recently proposed a model that can account for results favoring either eye-based or stimulus-based rivalry. In this two-stage model, competition occurs both at a monocular and binocular level of processing. Results traditionally in favor of the low-level view (e.g. Tong & Engel, 2001) occur at the monocular

level of competition. When suitable stimulus characteristics are used (for example, those used by Logothetis, Leopold and Scheinberg, 1996), competition at the monocular level can be eliminated, revealing rivalry at the binocular level.

Contextual modulation of binocular rivalry

An early study on contextual modulation of binocular rivalry was performed by Levelt (1965). Levelt surrounded one of two patches with a small annulus (0.5 deg in width). Based on his concept of stimulus strength, Levelt hypothesized that dominance of the target surrounded by the annulus would increase. Although dominance of the surrounded target increased, the increase was not significant. Later studies did show that surrounding stimuli modulated binocular rivalry significantly. For example, Fukuda and Blake (1992) repeated Levelt's experiment with larger surround stimuli and found that surrounding one target by an annulus lengthened its dominance duration. In a subsequent experiment, they surrounded orthogonally oriented rival gratings with annuli containing the same orientation as one of the two. This manipulation led to a significant *decrease* of dominance of the target with the *same* orientation. Fukuda and Blake (1992) proposed that this modulation of dominance was the result of surround interactions known from physiology. As discussed above, the response of a neuron selective for a certain orientation is often inhibited by presenting the same orientation outside its classical receptive field (e.g. Allman et al., 1985).

In a more recent study on rivalry between motion stimuli, Blake, Yu, Lokey and Norman (1998) surrounded targets containing moving dots with an annulus containing motion. The annulus surrounded one of the targets and could contain motion in the same direction or in the opposite direction to one of the targets, or contained random motion. In line with Levelt (1965) and Fukuda and Blake (1992), they found that the target surrounded by the annulus was most dominant. In addition, when target and surround contained motion in opposite directions, the increase was larger. Again, this finding points towards the involvement of center-surround interactions within center and surround regions of receptive fields of visual processing neurons.

In two papers, Alais and Blake (1998, 1999) discussed how binocular rivalry is affected by perceptual grouping. However, both studies are also informative on how binocular rivalry is affected by visual context. In one study, Alais & Blake (1998) used a four-aperture display containing motion. Although the four apertures contained motion in a different direction, the motions could be perceptually grouped into a single global motion direction. This stimulus was presented dichoptically. However, in one of the two sets (one presented to the left eye, the other to the right), one aperture contained static random dots, rivaling with the component motion grating presented to the other eye. There were two main results: when the component grating was suppressed, the global motion percept was diminished. On the other hand,

dominance of the component grating was increased when it was part of the global motion configuration.

In the second paper, Alais and Blake (1999) studied the influence of Gestalt principles – good continuation and common fate – on binocular rivalry. Good continuation refers to the effect that visual features will likely be perceived as a single object when they follow a common path (Wertheimer, 1923). The common fate principle applies to temporal and spatial changes in an array of features: when multiple features share the same temporal and spatial characteristics (they move with the same speed, in the same direction), they are perceived as belonging to one single object or pattern (Wertheimer, 1923). Alais and Blake (1999) presented multiple rival targets at different locations in the visual field. For example, two gratings were presented to the left eye at different positions. Random dots were presented at corresponding positions to the right eye. Joint predominance of the rival targets was higher when the orientations of the gratings were collinear than when they were orthogonal. To look at the role of common fate in binocular rivalry, the contrast of the rival gratings was modulated in time. When the contrast modulations of the rival targets correlated in time, joint predominance was increased.

Using binocular rivalry to study contextual modulation of visual perception

The previous discussion highlights that binocular rivalry can be modulated by visual context. Therefore, the following assumption is built upon throughout this dissertation: if visual context affects visual processing, the result of this modulation will be observable during binocular rivalry. As shown, changing an aspect of a stimulus engaged in binocular rivalry affects perceptual dominance of this stimulus. For example, decreasing contrast of a rival target will – according to Levelt (1965) – lower its stimulus strength, leading to increased perceptual dominance of the other rival target. Furthermore, the amount of change in dominance of a rival target is indicative of the relative change in strength of the rival target; a larger change in strength of a target will modulate perceptual dominance more than a smaller change in strength. Using this line of reasoning we can make hypotheses about contextual modulation: if adding a visual context increases dominance of target A, it can be inferred that the context decreased the strength of target B, or increased the strength of target A. Moreover, using Levelt's second proposition, the hypothesis can be made more explicit: if adding a context increases the dominance duration of target A, leaving that of B unaffected, it can be inferred that the context decreased the strength of target B.

Attentional modulation of binocular rivalry

Before turning to the findings reported in this dissertation, the role of visual attention in

visual perception is discussed. Psychologists often make the distinction between voluntary and involuntary attention, the former referring to the ability to voluntarily select a specific target from an array of stimuli, the latter referring to the fact that certain stimulus features appear to grab visual attention automatically (Desimone & Duncan, 1995). Within this general distinction, attention is thought to modulate spatial (Posner, 1980), object-based (Duncan, 1984) and feature-based (Treue & Martinez-Trujillo, 1999) processing. Regardless of theoretical perspective, allocating attention to a given aspect of a visual scene is assumed to improve visual processing of this aspect, reflected by improved performance on a relevant task. Recently, it has been observed that attention can increase the neural signal underlying some aspect of visual processing (e.g. Reynolds & Chelazzi, 2004). For example, attending to a specific direction of motion has been found to increase the neural response to stimuli sharing the direction of motion but presented elsewhere (Treue & Martinez-Trujillo, 1999). Also, attention has been found to modulate neural responses as early as the level of primary visual cortex (Gandhi, Heeger & Boynton, 1999).

Regarding the role of attention in binocular rivalry, the debate is more or less about whether rivalry is an automatic (also labeled bottom-up, or stimulus-driven) process or a process subject to voluntary (or top-down) control. As discussed, Helmholtz (1962) claimed he could voluntarily control rivalry. Helmholtz argued that by concentrating on some aspect of a rival target (for example, counting its lines), perceptual dominance was lengthened. However, he also admitted that attentional control was limited; a dominant target would eventually lapse into suppression. Helmholtz' observation was subsequently tested by Lack (1978) who showed that voluntary control over rivalry was possible after some training. Later, different paradigms have been employed to test various aspects of attention in relation to binocular rivalry. For example, Ooi and He (1999) employed a cueing paradigm and showed that spatial cueing could both prolong dominance of a target, and could increase the possibility of a target to become dominant. The authors argued that the former effect of attention was due to voluntary attention, whereas the latter was due to involuntary attention.

In a recent paper, Mitchell, Stoner & Reynolds (2004) showed that binocular rivalry can be modulated by object-based attention. Observers attentionally selected one of two superimposed transparent surfaces. When one of the surfaces was selected, the two surfaces were presented dichoptically, resulting in binocular rivalry. It was found that the surface that was perceptually dominant upon dichoptical presentation was often the one that had been attentionally selected. Mitchell et al. (2004) argued that this result indicates top-down control over binocular rivalry. Meng and Tong (2004) argued that attentional control over rivalry is limited. In their study, attentional control over several stimuli leading to bistable perception (the Necker cube and rival stimuli) was compared. Observers were for example instructed to "attempt to perceive the cube from the top view for as long as possible" (Meng & Tong, 2004, p. 541). When comparing dominance durations for attended and passively viewed stimuli, the

authors observed less attentional control over binocular rivalry as compared to the Necker cube. The authors concluded that, in contrast to the Necker cube, attentional control over binocular rivalry is limited, reflecting a low-level process underlying rivalry alternations.

Outline of the dissertation

In the following chapters, we systematically study the influence of visual context on visual perception using binocular rivalry. As mentioned, knowledge from neurophysiology will often be used to generate hypotheses about contextual modulation of visual processing at the level of perception. More specifically, the following questions are asked: How does visual context affect binocular rivalry? Can perceptual manifestations of center-surround interactions at the neural level be observed during binocular rivalry? If so, are these center-surround interactions a general property of visual processing, occurring for multiple stimulus-characteristics? At what levels of visual processing are center-surround interactions acting? Which aspects of a stimulus are affected by visual context? What is the contribution of visual attention in contextual modulation of visual processing?

Chapter 2 establishes that binocular rivalry is useful to study contextual modulation of visual perception. An experiment is discussed in which opposing rival motions were surrounded by motion in the same direction as one of the two rival targets. The surround motion lead to predominance of the opposite direction target. It is argued that this surround modulation is the perceptual manifestation of center-surround interactions at the neural level.

Chapter 3 discusses the generality of center-surround interactions using several stimulus characteristics. In a series of experiments, opposite-direction motion targets were surrounded by motion in the same direction as one of the two, orthogonal gratings were surrounded by the same orientation as one of the two, and red and green targets were surrounded by the same color as one of the two. Again, the results are supporting the hypothesis that center-surround interactions at the neural level are giving rise to modulations of perceptual dominance during binocular rivalry. Moreover, the results show that center-surround interactions are likely to be a general property of visual processing occurring for several stimulus characteristics, such as motion, orientation and color. Interestingly, center-surround interactions appear to be adaptive; depending on stimulus contrast, the surround increased or decreased the dominance of a target.

Chapter 4 describes how size and contrast of the visual context affects binocular rivalry, and at what level(s) of visual processing center-surround interactions act. Rivalry was instigated between a motion and a stationary target surrounded by motion in the same or in the opposite direction to the motion target. Perceptual dominance of the rival targets was compared for various sizes of surround motion and for several contrast levels of targets and surrounds. Perceptual dominance of the rival targets was dependent on all three factors

(direction of motion, surround size and contrast). Interestingly, the way by which a motion surround modulated binocular rivalry was in line with Levelt's (1965) second proposition. Adding same-direction motion to the surround of a motion and stationary target mainly increased dominance of the stationary target, leaving dominance of the motion target relatively unaffected. It is suggested that the motion surround affected stimulus strength of the motion target in a manner similar to lowering the luminance contrast of this target. Thus, center-surround inhibition appears to affect visual perception of a stimulus in a manner similar to lowering the contrast of this stimulus.

In the same chapter, evidence is provided for the notion that center-surround interactions occur at both monocular and binocular levels of visual processing. In an experiment *not* using binocular rivalry, ambiguous center motion presented to one eye only was surrounded by horizontal motion presented to the same eye only, or to the other eye only. Both types of stimulus presentations lead to a significant bias of perceived center motion direction: the center appeared to contain motion in the opposite direction to the surround. Again, this finding is indicative of center-surround interactions to be involved in visual motion processing. The results further provide support for the idea that center-surround interactions are active at multiple levels of visual motion processing.

In chapter 2 – 4, dominance durations were used to assess contextual modulation of binocular rivalry. Chapter 5 uses a different approach. During binocular rivalry, one stimulus is temporarily absent in conscious vision. However, since the stimulus is presented to an eye, one can ask what information is still available to conscious inspection, even though the stimulus is not consciously perceived. Chapter 5 shows that a motion pulse presented on a suppressed target is more difficult to discriminate when this target is surrounded by motion. The ability to discriminate was diminished even more when center target and surround moved in the same direction. This result adds evidence to the finding that a visual surround can modulate visual perception during binocular rivalry. Again, center-surround inhibition appeared to lower the strength of same-direction motion, in this case resulting in deeper suppression.

Chapter 6 discusses the role of visual attention in contextual modulation of visual perception. Again, binocular rivalry is used to investigate this question. Most studies have reported limited control over binocular rivalry. However, a problem in some of these studies is the lack of a task to quantify attention. This chapter provides a manner to quantify visual attention and its influence on binocular rivalry. The experiments reported here show that attention *speeds* binocular rivalry: attending away from binocular rivalry lengthened dominance durations. In addition, an explanation is given that might account for the lack of attentional control over binocular rivalry reported by earlier studies.

Chapter 2

Center-surround interactions in visual motion processing during binocular rivalry

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Abstract

When each of the two eyes is confronted with a dissimilar stimulus, the percept will generally alternate between the two. This phenomenon is known as binocular rivalry. Although binocular rivalry occurs for locations where targets overlap spatially, the area surrounding rivalrous targets can modulate their dominance. Here, we show that during binocular rivalry of oppositely moving gratings, a surrounding grating moving in the same direction as one of the two leads to increased dominance of the opposite direction of motion in the center. Inspection of the results for different conditions reveals that the preference for the opposite direction of motion cannot be explained by one single mechanism operating after binocular fusion. We therefore suggest that this phenomenology is the outcome of center-surround interactions at multiple levels along the pathway of visual motion processing.

Introduction

When dissimilar stimuli are presented at overlapping retinal locations of the two eyes, the percept periodically switches between the two. This phenomenon is known as binocular rivalry. Binocular rivalry is believed to occur at locally overlapping regions. This can be illustrated by the fact that large dissimilar stimuli lead to patch-like rivalry, whereas small dissimilar stimuli lead to periods of exclusive dominance of one entire stimulus (Blake, O'Shea & Mueller, 1992).

However, binocular rivalry is not just a local process. It is known that the area surrounding one of two rivalrous targets can modulate the dominance of the targets. The first systematic investigation of spatial interactions between central rivalrous stimuli and surrounding areas was performed by Levelt (1965). Levelt presented a black disc to one eye and a white disc to the other eye, resulting in rivalry. In one condition, a contour was added to one of the two discs. Levelt reasoned that adding a contour would increase the 'stimulus strength' of the disc, leading to increased dominance of the center disc surrounded by the contour. Levelt found that the predominance of the target surrounded by the contour increased, although this increase was not statistically significant. Later studies, however, did show that the area surrounding rivalrous targets could modulate rivalry significantly (Ichihara & Goryo, 1978; Mapperson & Lovegrove, 1991; Fukuda & Blake, 1992). In addition, Fukuda and Blake (1992) presented two patches containing orthogonally oriented bars that were both surrounded by an annulus containing bars with the same orientation as one of the two. In this condition, the patch containing bars with the orientation orthogonal to the surround was more dominant during rivalry.

The latter finding resembles results from physiological studies in cats and monkeys, which show that the response to an optimally oriented stimulus presented to a neuron's classical receptive field (CRF) in primary visual cortex can be inhibited by presenting a stimulus with the same orientation to its surround (e.g. Blakemore & Tobin, 1972; Knierim & van

Essen, 1992). In Fukuda and Blake's (1992) experiment, when orthogonally oriented bars are each surrounded by an annulus with the same orientation as one of the two, the center stimulus with the same orientation as the surround is expected to be inhibited by the surround. This would lead to a relatively higher 'stimulus strength' of the center bars surrounded by the orthogonally oriented surround, resulting in increased perceptual dominance of this center stimulus.

In motion sensitive neurons in middle temporal area (MT), center-surround interactions are also found. These interactions are often antagonistic, when the response to motion in the preferred direction of the CRF is inhibited by surround motion in the same direction (e.g. Allman, Miezin & McGuinness, 1985; Born & Tootell, 1992). Recently, Tadin, Lappin, Gilroy and Blake (2003) reported perceptual correlates of these center-surround interactions. They showed that detection thresholds increased with increasing size of a high-contrast drifting Gabor. They proposed that this increase in threshold was the perceptual manifestation of center-surround inhibition, presumably located within motion-sensitive area MT. Moreover, induced motion (or motion contrast), where a stationary stimulus is perceived to move in a direction opposite to the surround (Duncker, 1938; Reinhardt-Rutland, 1988), is believed to be another perceptual manifestation of this center-surround antagonism (Murakami & Shimojo, 1996).

The goal of this study was to investigate in what way center-surround interactions modulate binocular rivalry of motion stimuli. We used two center gratings moving in opposite directions. These center gratings were surrounded by an annulus containing a grating moving in the same direction as one of the two. Based on the findings on center-surround interactions in visual motion processing, we predicted that presenting motion in the surround would lead to increased stimulus strength of the center stimulus with the opposite direction of motion, leading in turn to increased perceptual dominance of this motion direction.

Methods

Observers

Six experienced observers participated in the experiments. Four of the observers were naïve as to the purpose of the experiments. The other two observers (CP & SP) are authors of the current paper. All observers had normal or corrected to normal vision.

Apparatus & Stimuli

The stimuli were generated by an Apple Macintosh dual 867 MHz G4 using the Psychtoolbox (Brainard, 1997; Pelli, 1997) and displayed on a luminance linearized 22" LaCie Blue

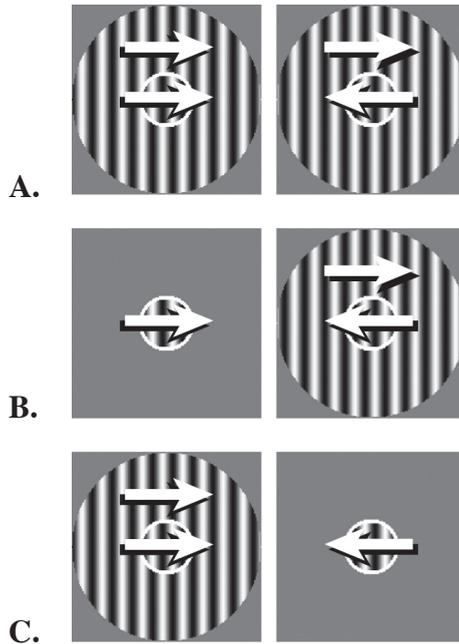


Figure 1. Stimuli and conditions used in the experiment. The arrows indicate the direction of motion of the gratings. The image on the left was presented to one of the two eyes, the right image to the other eye. A. The Binocular Surround (BS) condition. The surround was presented to both eyes. B. The Monocular Surround Opposite Same (MSOS) condition. The surround was presented around the grating with the opposite direction of motion. C. The Monocular Surround Opposite Other (MSOO) condition. The surround was presented around the grating with the same direction of motion. See text for details.

Electron monitor, at 85 Hz. The viewing distance was 72 cm. Dichoptical presentation was achieved by means of a stereoscope.

Stimuli and conditions are presented in Figure 1. Stimuli consisted of two circular apertures that could each be surrounded by an annulus. Both center and surround contained sine-wave gratings moving horizontally. The center gratings moved in opposite directions; the surrounding gratings moved in the same direction as one the center gratings. All gratings had a spatial frequency of 1.96 cycles/deg, moved with a constant speed of 1.27 deg/sec and were presented at 99% contrast. The mean luminance of both the gratings and the background was 50.1 cd/m². The diameter of the center aperture was 1.24 deg; the width of the surrounding annulus was 1.70 deg. There was a gap of 0.09 deg between the center aperture and the annulus. A white ring filling the gap between center and surround and a white square drawn around the annulus facilitated binocular fusion. The center apertures were presented in all conditions. We varied the positioning of the surround in four conditions:

1. Surround around both apertures (Binocular Surround (BS))
2. Surround around the aperture with the opposite direction of motion (Monocular Surround Opposite Same (MSOS))
3. Surround around the aperture with the same direction of motion (Monocular Surround Opposite Other (MSOO))
4. No surround (NS)

In all conditions, the directions of motion within the center apertures were counterbalanced between both eyes. Also, the direction of motion in the surround was counterbalanced between leftward and rightward motion. In the conditions where the surround was presented to one eye only, the positioning of the surround was counterbalanced between the two eyes. All conditions were presented in random order.

Procedure

During the experiments, observers sat in a dark room while a chin rest supported their head. Observers were instructed to fixate a central marker and to continuously indicate the perceived direction of motion in the center. Before starting the experiment, observers were familiarized with the stimuli and the task. At the beginning of a trial, the fusion guides appeared along with a fixation cross which remained present during the trial. The stimuli appeared 0.5 sec later. One trial lasted 30 sec. After the stimuli disappeared, a dynamic mask was presented for 4.5 sec to minimize motion adaptation effects (e.g. Anstis, Verstraten & Mather, 1998). One session lasted about 10 minutes. All observers performed 5 sessions, resulting in 20 trials per condition per observer.

Results

The results are presented in Figure 2. We used two measures to analyze the dominance of responses corresponding to the perceived direction of motion in the center. The first is cumulative dominance percentage, which represents the mean cumulative durations of both the opposite and same direction responses during one trial, expressed as the percentage of the total presentation time (Figure 2a). This measure is informative about the relative dominance of both the same and the opposite direction of motion. The second is mean dominance duration, which refers to the mean duration of both the opposite and same direction responses per trial (Figure 2b). This measure is informative about the way by which the surround modulates the dominance of the motion in the center. For example, it might reveal that when a surround is presented, the same direction of motion is perceived for shorter durations and the opposite direction for longer durations.

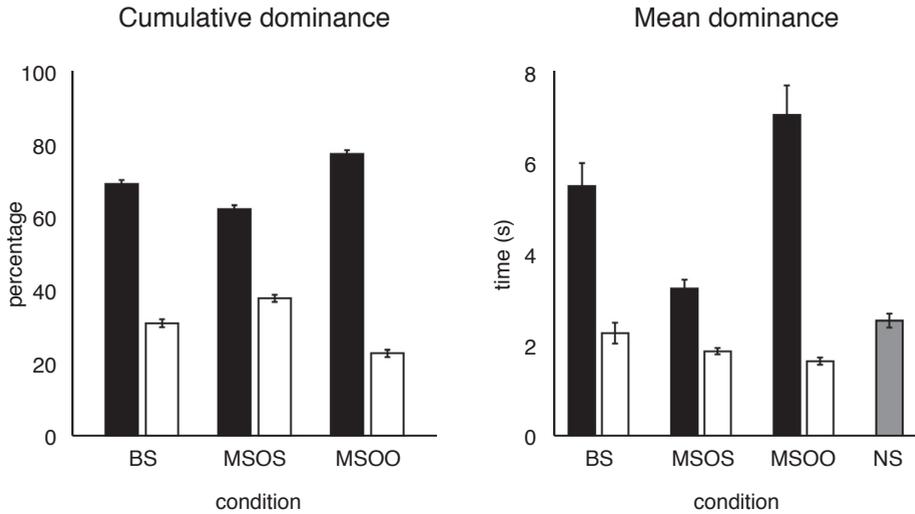


Figure 2. Results of the experiment. Results are averages of 6 observers. Grouped bars represent the different surround conditions. The black bars represent the dominance of the opposite direction of motion (compared to that of the surround); the white bars the dominance of the same direction. Standard errors of the mean are plotted on top of the bars. Left panel: Cumulative dominance percentage. Right panel: Mean dominance duration. The grey bar represents the data for the No Surround (NS) condition.

As can be seen from Figure 2a, the cumulative dominance percentage of the opposite direction of motion is larger than 50% percent in all conditions where surround motion was presented (BS: $T = 17.3$, $p < 0.001$, MSOS: $T = 12.3$, $p < 0.001$, MSOO: $T = 27.9$, $p < 0.001$). Figure 2a also shows that the different surround conditions yield different effect magnitudes. The preference for the opposite direction of motion is larger in MSOO than in BS ($T = 5.6$, $p < 0.001$), which in turn is larger than in MSOS ($T = 4.62$, $p < 0.001$). The difference between MSOO and MSOS is also significant ($T = 10.8$, $p < 0.001$).

From Figure 2b, one can appreciate that the mean dominance times are strongly modulated by surround motion. The mean dominance time of the opposite direction of motion is larger than that of the No Surround condition in all surround conditions (NS versus BS: $T = 5.6$, $p < 0.001$, NS versus MSOS: $T = 2.9$, $p = 0.01$, NS versus MSOO: $T = 6.8$, $p < 0.001$). In addition, the mean dominance time for the same direction of motion is decreased compared to that of the No Surround condition in the MSOS and the MSOO conditions (NS versus MSOS: $T = 4.0$, $p < 0.001$, NS versus MSOO: $T = 5.2$, $p < 0.001$), but not in the BS condition ($p > 0.05$).

Discussion

The results show that the opposite direction of motion is more dominant in all surround conditions. The opposite direction of motion appears to have high ‘stimulus strength’ during rivalry. This is illustrated by the fact that in some trials, observers exclusively perceived the opposite direction of motion during the entire presentation of 30 seconds. Apparently, the surround can strongly modulate the local rivalry process between the center gratings.

A related phenomenon was observed by Blake, Yu, Lokey and Norman (1998). They presented dots moving either rightward or leftward to the left and right eye, which in some conditions were surrounded by an annulus containing dots moving in the same direction, the opposite direction or in random directions. The results showed that the center stimulus that was surrounded by the annulus became more dominant, irrespective of the direction of motion within the annulus. This discrepancy with our results, however, might be due to that fact that Blake et al. used white dots on a black background, whereas we used sine-wave gratings on a background with the same mean luminance.

Blake & Logothetis (2002) suggested that the same ‘neural machinery’ is involved during perception of a dominant stimulus under rivalry conditions as in the case of normal, non-rivalrous viewing. Thus, center-surround interactions within visual processing stages under normal (non-rivalrous) viewing conditions are likely candidates to explain the results described here. Therefore, based on physiological studies on motion processing, it is tempting to suggest that the observed phenomenology is the result of center-surround interactions at the level of human MT/V5. Since center-surround interactions are often antagonistic, the preference for the opposite direction of motion during binocular rivalry could be the result of relatively lower stimulus strength for the center grating moving in the same direction as the surround. This in turn would increase the relative strength of the opposite direction of motion, resulting in increased perceptual dominance of this direction of motion.

Interestingly, most input to MT neurons is binocular. Accordingly, center-surround antagonism beyond the site of binocular fusion would explain the results. However, the results show that the preference for the opposite direction of motion is much larger in the MSOO condition compared to the MSOS condition. If inhibition of the same direction of motion would occur only after binocular fusion, both conditions should have yielded similar results. In this respect it is interesting to note that center-surround interactions in motion processing in V1 have been shown to resemble those found in MT (Jones, Grieve, Wang & Sillito, 2001). Therefore, it might be possible that center-surround interactions before the level of MT are also involved in the observed effects.

In conclusion, we find a strong preference for motion in a direction opposite to that in the surround during binocular rivalry. This implies that surround motion can modulate motion rivalry occurring locally. Although center-surround interactions after binocular fusion at

the level of MT are potent candidates to explain the results, it is likely that center-surround interactions at earlier stages of processing are also involved.

Acknowledgements

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Chapter 3

Adaptive center-surround interactions in human vision revealed during binocular rivalry

Article in press:

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Abstract

We used binocular rivalry as a psychophysical probe to explore center-surround interactions in orientation, motion and color processing. Addition of the surround matching one of the rival targets dramatically altered rivalry dynamics. For all visual sub-modalities tested, predominance of the high-contrast rival target matched to the surround was greatly reduced. This reduction of dominance of the matched target disappeared at low contrast. Even more so, at low contrast, adding the surround boosted dominance of orientation and motion targets. This contrast-dependent modulation of center-surround interactions seems to be a general property of the visual system and may reflect an adaptive balance between surround suppression and spatial summation.

Introduction

The response of a neuron to a specific stimulus feature presented to its classical receptive field is often affected by presenting the same feature to its (non-classical) surround (Allman, Miezin & McGuinness, 1985; Born & Tootell, 1992; Tanaka, Hikosaka, Saito, Yukie, Fukada & Iwai, 1986). The nature of these surround interactions is often inhibitory: presenting same direction motion to the surround of a neuron's receptive field often reduces the response to motion presented to the center. It has been argued that such surround inhibition is implicated in figure-ground segregation (Born, Groh, Zhao & Lukasewycz, 2000), optimizing information transmission (Vinje & Gallant, 2000) and perception of surface shape (Buracas & Albright, 1996). However, surround suppression might become problematic when neural response to a stimulus is already weak, for example when stimulus visibility is low. Recent research indicates that this potential problem can be circumvented by reducing surround suppression and/or increasing spatial summation at low contrast (Sceniak, Ringach, Hawken & Shapley, 1999; Pack, Hunter & Born, 2005; Tadin, Lappin, Gilroy & Blake, 2003). For example, in area MT, the suppressive influence of the surround is abolished or greatly attenuated at low contrast (Pack et al., 2005). Does this flexibility at the single neuron level reveal itself at the level of perception? Moreover, are such adaptive surround interactions a general property of visual processing?

Using binocular rivalry as a tool, we addressed these questions by studying contrast-dependency of center-surround interactions in motion, orientation and color processing (Figure 1). Binocular rivalry was chosen for several reasons: The dynamics of perceptual alternations during binocular rivalry are indicative of the relative perceptual strengths of the rivaling stimuli (Levelt, 1965). Moreover, binocular rivalry is affected by changes in the surrounding visual context (Paffen, te Pas, Kanai, van der Smagt & Verstraten, 2004; Carter, Campbell, Liu & Walls, 2004; Alais & Blake, 1998; Fukuda & Blake, 1992; Sobel & Blake, 2002), in a manner that is generally in accord with known neurophysiology of contextual modulations.

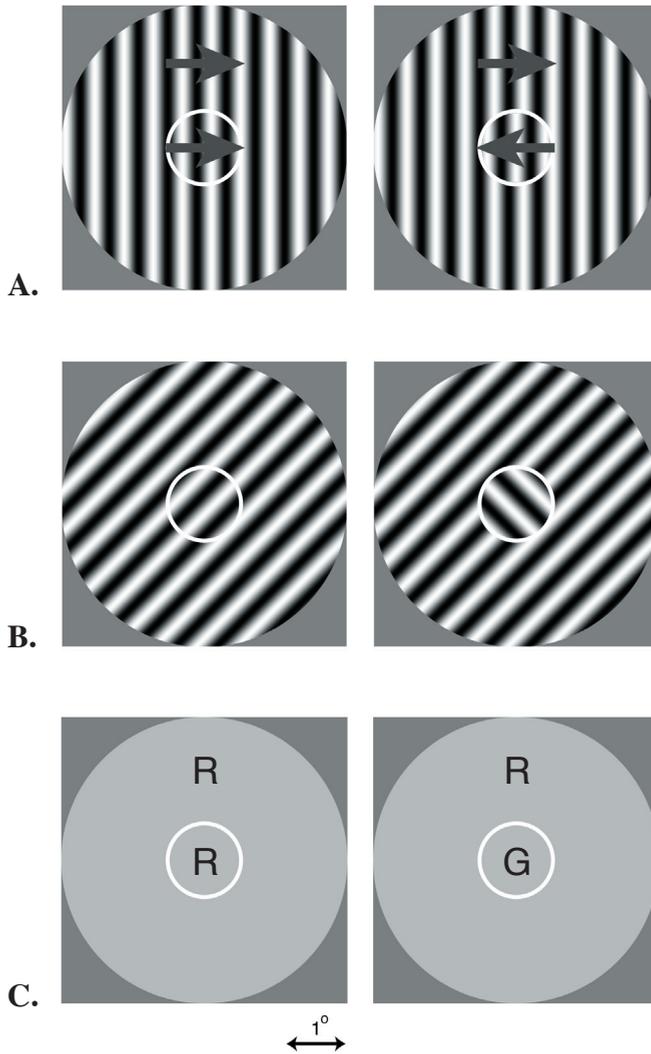


Figure 1. Examples of stimuli used in Experiment 1. A. Rival targets containing horizontal motion in opposite directions were surrounded by annuli containing gratings moving in the same direction as one of the targets. B. Rival targets containing orthogonal orientations were surrounded by annuli containing gratings with the same orientation as one of the targets. C. Red (R) and green (G) rival targets were surrounded by annuli containing the same color as one of the two targets.

For example, several studies hinted on surround interactions modulating dominance of center rival targets (Paffen et al., 2004; Carter et al., 2004; Fukuda & Blake, 1992). We capitalize on this contextual susceptibility of binocular rivalry in our effort to investigate adaptive center-surround interactions in three key attributes in human vision. Thus, by measuring changes in binocular rivalry when the surrounding stimulus was present, we seek to reveal the nature of center-surround interactions for different visual stimuli. Moreover, the use of binocular rivalry as an investigational tool allows us to employ equivalent experimental designs in different visual sub-modalities.

Methods

Stimuli are presented in Figure 1. Stimuli were generated in MATLAB using the Psychophysics toolbox (Brainard, 1997; Pelli, 1997). All rival targets were 1.2° in diameter. Surround annuli were presented binocularly and were 1.7° wide. A 0.1° gap separated center and surround. With the exception of the low-contrast color condition, the background was iso-luminant to the mean luminance of targets and surrounds. Mean luminance was 29 cd/m^2 for the motion experiment and 33 cd/m^2 for the orientation and color experiments. For the low-contrast color condition, the background was uniform black, to prevent color induction in the surround.

Motion stimuli were horizontally drifting sinusoidal gratings (spatial frequency = 2.0 cycles/deg , temporal frequency = 2.5 Hz). Contrast was either 100% or 1.5% (Michelson). Center rival targets contained motion in opposite directions and the binocularly presented surround contained motion in the same direction as one of the targets. Oriented stimuli had a spatial frequency of 2.0 cycles/deg and were slowly counterphasing (1 Hz) to prevent Troxler fading (Troxler, 1804). Contrast was either 100% or 1.7%. Center rival targets had orthogonal orientations (-45° and 45° from vertical), the surround orientation matched one of the rival targets. Chromatic targets and surrounds were red and green patches presented at perceptual iso-luminance. Iso-luminance was achieved by running a flicker-matching procedure at 12.5 Hz before each session. Center and surround were presented either at high color contrast (36% Michelson in xy color space (Vos, 1978)), or at low color contrast (2%). At high color contrast, the surrounds had the same chromaticity as one of the two targets. For low contrast conditions of all experiments, we checked whether observers were able to discriminate between the two rival targets by running several discrimination-threshold staircases. Discrimination thresholds of all observers were well below the contrast values used in the rivalry experiments.

Rival targets were presented dichoptically using a mirror stereoscope. Viewing distance was 95 cm for motion conditions and 72 cm for all other conditions. Left- and right-eye stimuli were surrounded by high-contrast guides to promote binocular fusion. Motion and orientation stimuli were presented for 45 s , color stimuli for 30 s . During that time, observers continuously indicated their dominant percept by pressing one of two keys. Six main condi-

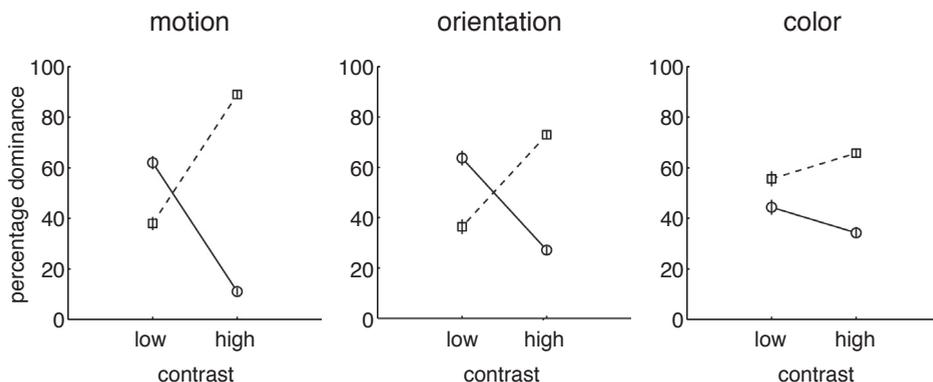


Figure 2. Results of Experiment 1. Average percentage dominance as a function of contrast is shown for rival targets defined by motion direction (left panel), grating orientation (middle panel) and color (right panel). Solid lines and circles show cumulative dominance for the target sharing its defining feature with the surround. Dashed lines and squares show the data for the target with the contrasting feature. Error bars represent standard errors of the mean.

tions (3 visual modalities at 2 contrasts) were run in separate blocks. For each main condition, all possible combinations of center features, surround features and eye presentation were investigated in random order, yielding 16 sub-conditions per observer. Five observers performed in the motion part of the experiment, four in orientation and color parts. In all conditions, three observers were naïve to the purpose of the study.

Results

For high-contrast rival motion targets and surrounds (Figure 2, left panel), dominance of the same direction rival target was greatly reduced. For low contrast targets and surrounds, however, the opposite result was observed: the same direction target was dominant most of the time. Examination of dominance percentages reveals that reducing stimulus contrast (while keeping other parameters constant) results in a remarkable 6-fold increase in dominance of the surround-matched target. For stimuli defined by orientation (Figure 2, middle panel), the same orientation rival target was mostly suppressed at high contrast, but exhibited increased dominance at low contrast. In accord with motion and orientation findings, at high color contrast (Figure 2, right panel), dominance of the target matched to the surround was strongly reduced. When color contrast was reduced, there were no significant biases in dominance (Wilcoxon Signed Ranks test: $T = 777$, $n = 64$, $p = 0.08$). Note that although color results did not “flip” as observed for motion and orientation, the direction of the effect was same in all conditions.

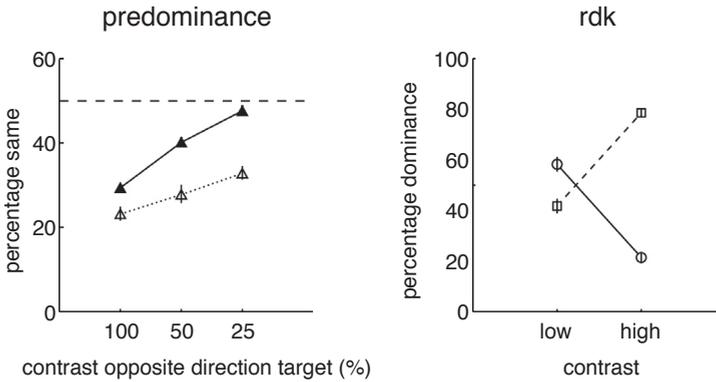


Figure 3. Results of Experiment 2 and 3. Left panel: Average percentage predominance of the target sharing its defining feature with the surround across several contrasts of the contrasting target. Solid lines and filled triangles represent predominance for static targets, dotted lines and open triangles data for motion targets. The dashed line represents the level at which predominance of the rival targets is in balance. Right panel: Average percentage predominance of random pixel motion as a function of contrast. Solid lines and circles show cumulative dominance for the same direction motion, Dashed lines and squares show the data for opposite direction motion. Error bars are standard errors of the mean.

The results from the first experiment suggest that the presence of high-contrast surrounds reduces the “strength” of the target matching the surround. In order to test this hypothesis, we performed an experiment in which we varied the contrast of the target not matching the defining feature of the surround. If a high contrast surround lowers the strength of a central target with the same defining feature as the surround, lowering the strength of the target with the contrasting feature (by lowering its contrast) should reduce predominance of the contrasting target. CP and a naïve observer participated in an experiment in which motion and orientation stimuli were used similar to those of the first experiment, except that the contrasting target was presented either at 100, 50 or 25% luminance contrast.

Predominance of the target matching the defining feature of the surround increased with decreasing luminance contrast of the contrasting target (Figure 3, left panel). In addition, predominance increase was larger for oriented targets than for motion targets. Note that predominance of the same direction motion target is about 30% at 25% contrast of the opposite direction target, whereas predominance of the same orientation target is about 50% at the same contrast level. Thus, in contrast to a same orientation target, surround inhibition of a same direction motion target is still quite strong at 25% luminance contrast, suggesting that surround influence is stronger and more resistant for motion targets (also compare motion and orientation conditions of Figure 2). This observation may stem from the faster contrast saturation of the motion system (Sclar, Maunsell & Lennie, 1990) and/or the fact that the orientation

of the rival motion targets matched the surround orientation (Figure 1a).

In fact, the surround modulation for motion targets might in part be induced by the iso-oriented surround. To isolate surround interactions solely induced by a motion surround, we conducted an experiment in which rival targets and surrounds were replaced by random pixel arrays, which are broadband in terms of orientations present. Two naive and one author (CP) performed in this experiment of 16 trials per condition. Again, same direction dominance was greatly reduced at high contrast (100% Michelson), and boosted at low contrast (3% Michelson) (Figure 3, right panel).

Discussion

We show that when rival targets are of high contrast, a target matching the surround in the relevant visual attribute is effectively weaker than a target that differs from its surround. In principle, this result could arise from surround facilitation of the target differing from the surround or from surround suppression of the target matching the surround. From the rivalry data alone, we cannot distinguish between these two possibilities as both predict similar changes in predominance. Neurophysiological investigations, however, primarily report strong and widespread suppressive interactions in motion (Born & Tootell, 1992; Tanaka et al., 1986; Born et al., 2000), orientation (Jones, Wang & Sillito, 2002) and color processing (Solomon, Peirce & Lennie, 2004). True facilitation (response above the response to the optimal center stimulus alone), however, occurs only in a portion of neurons (Tanaka et al., 1986; Jones, Grieve, Wang & Sillito, 2001; Jones et al., 2002; Series, Lorenceau & Fregnac, 2003). Moreover, we have previously shown that surround suppression has pronounced effects on motion perception (Tadin et al., 2003). In addition, we have observed that the effects reported here are reduced if the center and surround gratings in the “same” condition are out of phase (data not shown) — a manipulation that does not change the relationship between the center and the surround in the “opposite” condition. Thus, we are inclined to believe that center-surround interactions in binocular rivalry reported here likely arise from suppressive interactions. Such suppressive interactions may decrease neural response to the target matching the surround and presumably shift predominance balance in favor of the target differing from the surround.

On the other hand, when rival targets were of low contrast, predominance of the target matched to the surround increased. This contrast-dependent change of rivalry dynamics is consistent with recent work demonstrating that surround inhibition weakens or even changes to spatial summation as the stimulus visibility decreases (Sceniak et al., 1999; Tadin et al., 2003; Pack et al., 2005). Thus, contrast-dependent changes in center-surround interactions at the single neuron level are in accord with the contrast-dependent changes in binocular rivalry reported here. The absence of a boost in dominance for low-contrast color might be due to the fact that the contrast used was relatively high (2% in xy -color space, compared to 1.5 and

1.7% for motion and orientation respectively). However, at lower color contrast, observers were not able to track rivalry alternations.

In addition to demonstrating center-surround interactions, our results add to the evidence pointing to potent contextual modulation of binocular rivalry predominance. Among those sources of evidence are several earlier studies (Paffen et al., 2004; Carter et al., 2004; Alais & Blake, 1998; Fukuda & Blake, 1992; Sobel & Blake, 2002) showing that the global configuration in which a rival target is embedded can influence predominance of that target. None of those earlier studies, however, were conducted in ways that would have revealed the contrast-dependent complexities of the surround effects highlighted in the present study.

The contrast-dependent center-surround interactions modulating binocular rivalry are likely a general property of visual processing, as suggested by our observations in motion, orientation and color processing. Our results are not specific to binocular rivalry, for analogous results are seen in motion perception as indexed by duration thresholds and the motion after-effect strength (Tadin et al., 2003). Such flexible, stimulus-driven processing is clearly adaptive, because computationally powerful surround inhibition is only useful when neural signals are strong enough to withstand suppression. When signals are weak, however, it makes sense to boost those signals by summing interactions. We speculate that these adaptive surround interactions equip the visual system with a powerful tool to process visual information under a variety of visibility conditions.

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Chapter 4

Center-surround inhibition and facilitation as a function of size and contrast at multiple levels of visual motion processing

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Abstract

Visual context often plays a crucial role in visual processing. In the domain of visual motion processing, the response to a stimulus presented to a neuron's classical receptive field can be modulated by presenting stimuli to its surround. The nature of these center-surround interactions is often inhibitory; the neural response decreases when the same direction of motion is presented to center and surround. Here we use binocular rivalry as a tool to study center-surround interactions. We show that magnitude of surround suppression varies as a function of luminance contrast and surround width. Increasing the size of surround motion increased surround suppression at high contrast. Furthermore, large, high-contrast surrounds facilitated opposite direction motion in the center. For stimuli presented at low contrast, surround suppression peaked at a smaller surround width. In addition, we provide evidence that surround inhibition occurs at multiple levels of visual processing: surround inhibition in motion processing is likely to originate from both monocular and binocular processing stages.

Introduction

Since the pioneering work of Hubel and Wiesel (e.g., 1968), it is generally acknowledged that visual processing neurons respond selectively to specific stimulus features presented to their receptive fields. According to the classical concept of a receptive field, a neuron responds within a spatially restricted representation of the visual field (Hartline & Graham, 1932). However, many studies have shown that the response of such a neuron can be affected by simultaneously presenting stimuli outside its classical receptive field (e.g., Allman, Miezin, & McGuinness, 1985; Gilbert & Wiesel, 1990).

Center-surround interactions have been studied extensively in the domain of visual motion processing. The predominant nature of these center-surround interactions is inhibitory; the response to motion presented to the center of a neuron's classical receptive field decreases when the same direction of motion is presented to its non-classical surround (e.g., Allman et al., 1985; Raiguel, van Hulle, Xiao, Marcar, & Orban, 1995). In addition, facilitation of the neural response has also been reported (Allman et al., 1985; Born & Tootell, 1992). In this case, the neural response to center motion increases when motion is presented to the surround. The difference between the natures of surround interactions (inhibition vs. facilitation) might lie in the fact that different cells in MT show different behavior. As pointed out by Born and Tootell (1992), depending on where the cells are located within MT, some cells show facilitation of their response, others inhibition.

At the neuroanatomical level, surround interactions are often associated with motion selective area MT/V5 (e.g., Allman et al., 1985; Raiguel et al., 1995), although they are also observed at other levels involved in visual motion processing, such as V1 and MST (Jones, Grieve, Wang, & Sillito, 2001; Eifuku & Wurtz, 1998).

Several authors have proposed a functional role for center-surround interactions. Nakayama and Loomis (1974) predicted that center-surround interactions in motion processing play an important role in the detection of motion discontinuities or motion boundaries. In

addition, these interactions have been implicated in figure/ground segregation (Allman et al., 1985; Lamme, 1995), computation of self-motion during eye movements (Warren, 1995), and the construction of three-dimensional object shape (Koenderink & van Doorn, 1992).

Here we use binocular rivalry as a tool to study surround interactions. During binocular rivalry, dissimilar stimuli presented dichoptically compete for perceptual dominance (for reviews, see Alais & Blake, 2005, or Blake & Logothetis, 2002). Recently, we have reported evidence for center-surround interactions in motion processing during binocular rivalry (Paffen, te Pas, Kanai, van der Smagt & Verstraten, 2004). We dichoptically presented targets containing motion in opposite directions, which could each be surrounded by motion in the same direction as one of the two. Presenting surround motion increased the dominance of the center target containing the opposite direction of motion. Hypothetically, the increased dominance of the opposite direction of motion could be the result of surround facilitation of the opposite direction of motion, surround inhibition of the same direction, or a combination of both. However, because the center targets moved either in the same or in opposite direction as the surround in that experiment, it was not possible to disentangle surround inhibition from surround facilitation.

The goal of the first experiment of this study was twofold: (1) to disentangle surround inhibition from facilitation during rivalry and (2) to study the effect of varying the size of the surround and contrast of both the center and surround on the dominance of rival targets. Recently, both psychophysical (Tadin, Lappin, Gilroy, & Blake, 2003) and physiological (Pack, Hunter, & Born, 2005) studies have shown that magnitude of surround inhibition varies as a function of size and contrast of a motion stimulus. In general, increasing the size and contrast of a motion stimulus increases the magnitude of surround inhibition (Tadin et al., 2003).

In our second experiment, we investigated at what levels of processing center-surround interactions act. As discussed, neurophysiological studies have pointed toward several neuro-anatomical loci of center-surround interactions. We use a psychophysical approach to study levels of processing. More specifically, we ask whether processing levels before as well as after binocular fusion are involved in center-surround interactions. Many studies have looked into the contribution of monocular and binocular processing levels to various forms of visual motion processing (e.g., de Weert & Wade, 1984; Georgeson & Shackleton, 1989; Meng, Chen, & Qian, 2004). Here we study the role of monocular and binocular processing levels in surround interactions.

Experiment 1

The first goal of this experiment was to disentangle surround inhibition from surround facilitation during binocular rivalry. To achieve this, we modified the stimuli used by Paffen et al. (2004). In that experiment, rival targets containing opposite directions of motion were

surrounded by motion in the same direction as one of the two. To disentangle surround inhibition and facilitation, we replaced one rival target by a stationary target. The dominance of the stationary target will not depend on the direction of motion of the surround. To study surround inhibition, the targets were surrounded by motion in the same direction as the motion target. This manipulation should lead to decreased dominance of motion in the center. Absence of surround inhibition should leave dominance of the rival targets unaffected. Likewise, surround facilitation might be observed when both targets are surrounded by a direction of motion opposite to that of the motion target. In this case, the dominance of motion in the center should increase. Again, absence of surround facilitation should leave the dominance of the targets unaffected.

Second, to study the effect of size and contrast on surround interactions, we used four surround widths and three contrast levels of center and surround. Based on findings by Tadin et al. (2003) and Pack et al. (2005), we expected surround inhibition to increase with increasing size and contrast.

Methods

Observers

Four observers performed in this experiment. Two observers were naive to the purpose of the experiments. The other two were authors. All observers had normal or corrected-to-normal vision.

Apparatus & stimuli

The stimuli were presented with an Apple Macintosh dual 867 MHz G4 using the Psychtoolbox (Brainard, 1997; Pelli, 1997) and a single, luminance-linearized, 22" LaCie Blue Electron monitor at 85 Hz. Viewing distance was 72 cm. Dichoptic presentation was achieved by means of a mirror stereoscope.

The basic stimuli are presented in Figure 1. The stimuli consisted of two circular apertures that could each be surrounded by an annulus. Because a surround containing motion can possibly inhibit the response to a stationary target with the same orientation, we used a circular stationary concentric target instead. This target contained no motion or orientation information, enabling us to look at the effect of same- and opposite-direction surround motion on the rival motion target only. Although a motion surround is expected to modulate dominance duration of the motion as well as the static target, the source of this modulation will be the surround interactions between the motion surround and motion target. Thus, rivalry was instigated between a motion and a stationary target. The spatial frequency of the stationary

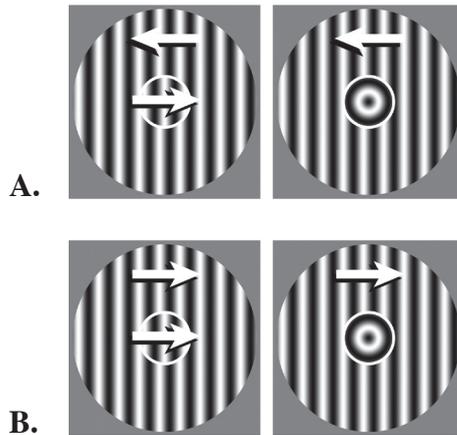


Figure 1. Typical stimuli as used in experiment 1. The stimulus on the left was presented to the left eye, the one on the right to the right eye. Arrows indicate the direction of motion of the grating. A. represents an opposite direction surround, B. a same direction surround.

target was matched to that of the motion target. The rival targets were each surrounded by an annulus containing a grating moving horizontally in the same or in the opposite direction as the motion target. The gratings had a spatial frequency of 1.96 cycles/deg and moved at a constant speed of 1.27 deg/s. The mean luminance of both the gratings and the background was 33 cd/m². The diameter of the center targets was 1.24 deg. The surround could have one of three widths (0.8, 3, or 6 deg) or could be absent. There was a gap of 0.09 deg between the center aperture and the annulus. Michelson contrast of both center and surround was 5.0, 49.8, or 99.7%. Binocular fusion was aided by fusion guides consisting of a white ring filling the gap between center and surround, a white square drawn around the annulus, and a central fixation marker.

Results

The results are presented in Figure 2. Because we expressed cumulative dominance of rival targets as percentages of total presentation time, we performed an arc-sine transformation on percentages to approximate normally distributed data. Next, we subtracted cumulative dominance of the motion target in the no-surround condition from its cumulative dominance in each of the surround conditions. As a result, negative values indicate a decrease and positive values indicate an increase in predominance of the motion target. Note that the data for the stationary rival targets are symmetrical – performing the same transformation on cumulative dominance of the static target (arc-sinus transformation followed by no-surround, surround

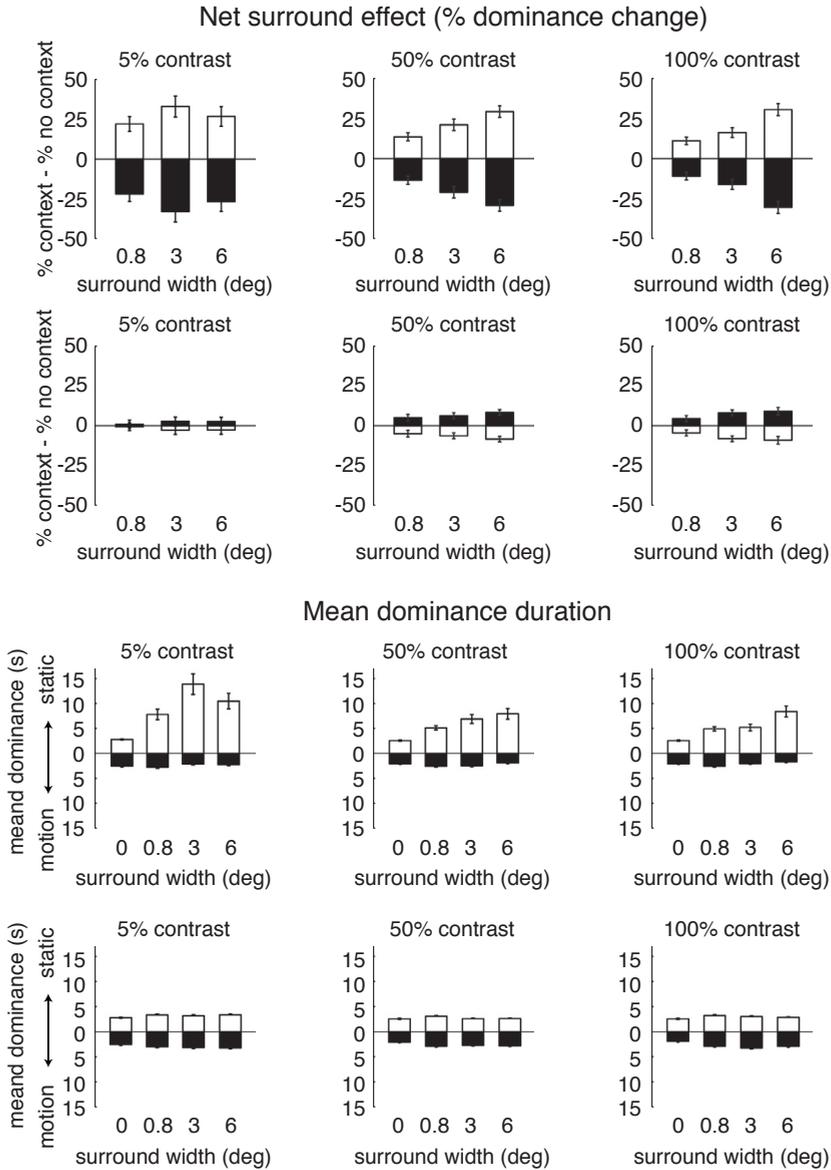


Figure 2. Results of experiment 1. Dominance of the motion and the static target for same and opposite surround motion at different surround sizes and contrasts. Results are pooled data for four observers. White bars represent dominance for the static target, black bars dominance for the motion target. The two upper panels plot the net effect in cumulative dominance of adding surround motion to the rival targets (see text). The two lower panels shows mean dominance durations. Error bars represent standard errors of the mean.

subtraction) gives the same data, but with opposite sign.

Next, we analyzed whether adding same-direction motion decreased cumulative dominance of the motion target (indicating inhibition), and whether opposite direction increased dominance (indicating facilitation). For all same-direction surrounds, dominance of the motion target was significantly smaller than zero, indicating inhibition (smallest, $T(31) > 4.5$; largest, $p < .001$). For opposite direction surrounds, only the two largest surround sizes for 50% and 100% contrast lead to significant increase of dominance of the motion target (smallest, $T(31) > 3.4$; largest, $p < .001$).

Next, we analyzed the influence of increasing size of surround and contrast of center and surround on predominance of the motion target. Applying a repeated measurements ANOVA with all factors (same and opposite direction surround, three surround widths, and three luminance contrasts) resulted in significant main effects of surround motion direction, $F(1,31) = 172.0$, $p < .001$, and surround width, $F(2,30) = 5.5$, $p = .006$, as well as significant interactions between surround motion direction and surround width, $F(2,30) = 14.5$, $p < .001$, and between surround motion direction, luminance contrast, and surround width, $F(4,28) = 3.1$, $p = .02$.

To understand the influence of size and contrast on each surround-motion direction, we analyzed the two motion directions separately. For same direction surround motion, we observed a significant main effect of surround width, $F(2,30) = 11.1$, $p < .001$, and a significant interaction between luminance contrast and surround width, $F(4,28) = 3.4$, $p = .01$. Figure 2 shows that increasing the size of the surround decreases the dominance of the motion target at 50% and 100% contrast. However, at 5% contrast, dominance durations show an U-shape with increasing size. Note that there is no overall increase in dominance of the motion target with increasing contrast.

For opposite direction surround motion, a significant main effect of surround width was observed, $F(2,30) = 4.5$, $p = .02$; increasing the width of the surround increases dominance of the motion target.

Discussion

The results of Experiment 1 can be summarized as follows. For large surround widths at high contrast, we find surround facilitation of the opposite direction of motion. At smaller sizes and low contrast, no facilitation of the opposite direction was observed.

For all same-direction surround conditions, we find evidence for inhibition. Increasing surround width decreased dominance of the motion target at 50% and 100% contrast. At the lowest contrast, adding a surround also decreased dominance of the motion target. However, maximum modulation is observed at a surround width of 3 deg. Thus, for the lowest contrast, surround inhibition appears to peak at a smaller size than at higher contrasts of center and surround.

Also, it can be noted that inhibition is generally stronger than facilitation; same direction motion had a stronger effect on dominance of the rival targets than opposite direction motion.

Our results are in line with Tadin et al. (2003), who used similar stimulus sizes (widths of 1 – 5 deg) and with Pack et al. (2005), who used stimuli up to 35 deg in diameter. These studies also reported evidence for increase of inhibition for high-contrast stimuli with increasing stimulus size. Our results on the effect of contrast are not as clear-cut. Whereas Tadin et al. (2003) reported an increase of duration thresholds and hence an increase in surround inhibition with increasing contrast, we find equal inhibition across several contrasts. On the other hand, the difference between duration thresholds of the two highest contrasts used by Tadin et al. (46% and 92%) was small. Also, as indicated by the significant interaction between surround width and contrast, surround inhibition does not increase for all sizes at the lowest contrast we used. Apart from this, we do not find much difference between magnitude of inhibition and level of luminance contrast. At 5% contrast, surround inhibition still appears to be quite strong. However, inhibition reaches its optimal level at a smaller size than at higher contrasts, which indicates that surround inhibition decreases with size at low contrast. A possible reason for the discrepancy between Tadin et al. (2003) and our data might be that they used a moving Gabor in their experiments, whose luminance contrast peaks at the center and drops in the periphery. The strong inhibition we find at the lowest contrast might be because luminance contrast of our surround was higher than that of Tadin et al. (2003).

Experiment 2

In Experiment 2, we did not use binocular rivalry to study surround interactions. Instead, we presented the center and surround to one eye only. The surround could be presented to the same eye as the center, or to the other eye. In this way, we can disentangle the respective contribution of monocular and binocular levels of processing to center-surround interactions.

We used a center target consisting of oppositely moving gratings with variable contrast ratio for leftward and rightward motion. Based on the results of Experiment 1, we predicted that adding a surround containing leftward or rightward motion would lead to a shift in the perceived direction of the center target toward a direction of motion opposite to that of the surround. In theory, binocular surround interactions can occur for both within- and between-eye presentation. However, monocular surround interactions can only occur for within-eye presentation.

For this experiment, several predictions can be made: If within-eye presentation of center and surround leads to a larger shift than between-eye presentation, it implies the contribution of monocular levels of processing. On the other hand, if only binocular levels are involved, both conditions should lead to a similar shift in the perceived direction of motion. In the ex-

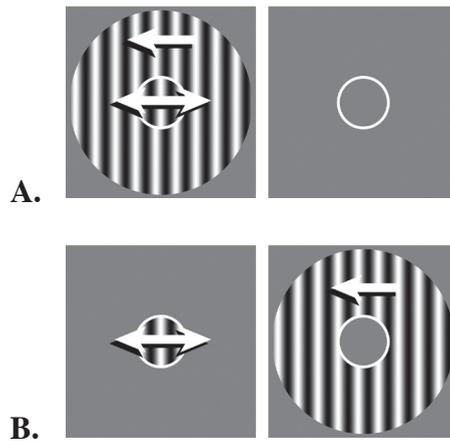


Figure 3. Stimuli and conditions used in experiment 2. In each condition, the center and the surround were presented to one eye only. The surround was presented either to the same eye as the center (A) or to the other eye (B).

treme case of absence of binocular components, only within-eye presentation should bias the perceived direction of motion in the center.

Methods

Observers

Five observers performed in this experiment. Three observers were naive to the purpose of the experiments. All observers had normal or corrected-to-normal vision.

Apparatus & stimuli

The set-up was the same as in Experiment 1. The stimuli and conditions are presented in Figure 3. The center stimulus was produced by adding a leftward and a rightward motion grating with variable contrast ratio. The surround moved either leftward or rightward. The diameter of the center targets was 1.24 deg; the surrounding annulus was 1.70 deg wide. There was a 0.09 deg gap between the center aperture and the annulus. The speed and spatial frequency of component center gratings and surrounding gratings were the same as in Experiment 1. The same holds for the mean luminance of stimuli and background. The experiment involved two conditions, a monocular surround condition and an interocular surround condition.

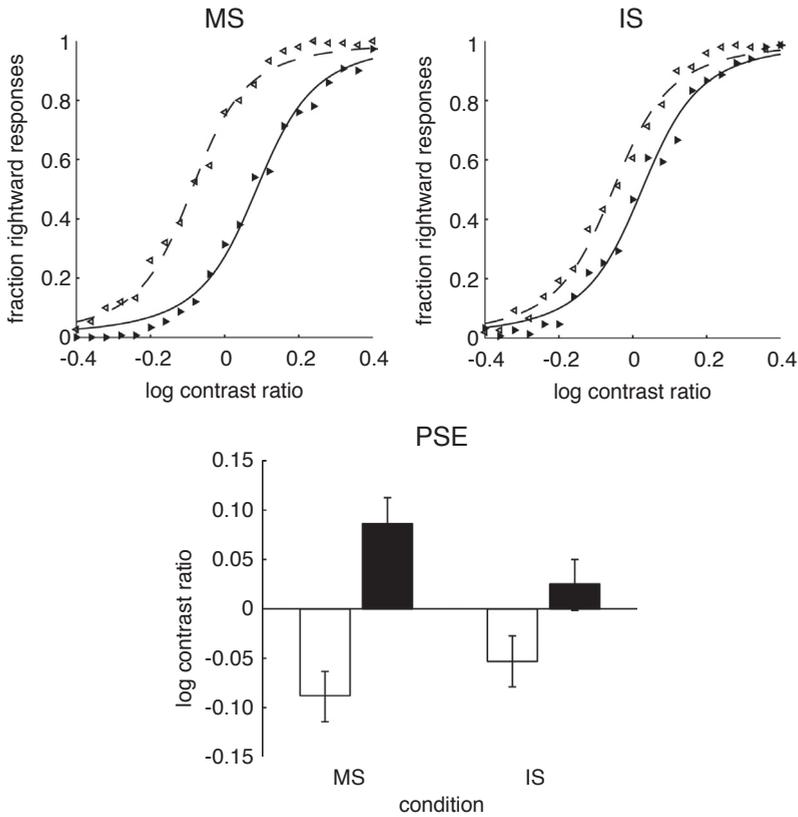


Figure 4. Results of experiment 3 for pooled data of five observers. Upper panels represent fractions of rightward responses plotted against the log contrast ratio of the center target (left/right). Triangles represent the fraction right responses for each of the contrast-ratios. Lines represent the psychometric curves resulting from fitting the data to a cumulative Gaussian. Filled triangles and solid lines represent the data for a rightward motion surround. Open triangles and dotted lines represent the data for leftward surround motion. The left and right panel represent the monocular (MS) and interocular surround (IS) condition respectively. The lower panel represents PSEs and 95% CIs for MS and IS conditions. White and black bars represent PSEs for leftward and rightward surrounds respectively.

Procedure

We varied the contrast ratio of the center stimulus using a constant-stimuli design. For each of the two conditions, we counterbalanced the positioning of the center grating (left eye, right eye) and the direction of motion of the surround grating. The observer initiated a trial by pressing the space bar. After 0.5 s, the stimuli were presented for 0.5 s. The task of the observer was to report the perceived direction of motion in the center. Each observer performed

| | MS-l | MS-r | IS-l | IS-r |
|------------|-------------|------------|-------------|-------------|
| CP | -0.04:0.01 | 0.04:0.08 | -0.08:-0.04 | -0.04:0.00 |
| EO | -0.07:-0.02 | -0.03:0.02 | -0.04:0.01 | -0.02:0.03 |
| MN | -0.10:-0.05 | -0.02:0.01 | -0.08:-0.01 | -0.12:-0.08 |
| OJ | -0.16:-0.11 | 0.20:0.25 | -0.11:-0.06 | 0.14:0.18 |
| SP | -0.18:-0.14 | 0.17:0.22 | -0.08:-0.03 | 0.08:0.13 |
| All | -0.11:-0.06 | 0.06:0.11 | -0.08:-0.02 | 0.00:0.05 |

Table 1. 95% confidence intervals of PSEs for all observers and the pooled data (all). MS-l and MS-r refer to the fraction rightward responses in the monocular surround condition for leftward and rightward surround motion respectively. IS-l and IS-r refer to the fraction rightward responses in the interocular surround condition for leftward and rightward surround motion respectively.

in 4 runs of approximately 10 minutes, resulting in 20 trials per contrast ratio.

Results

The results are presented in Figure 4 and in Table 1. For each of the conditions, we fitted all “rightward” responses against the log contrast ratio of the center stimulus. Values less than zero represent net leftward motion energy (when the log rightward-leftward-motion ratio is smaller than 1); values above zero represent net rightward motion energy. Psychometric functions (Figure 4, top panels) were acquired by fitting the data to a cumulative normal distribution function. From this function, the point of subjective equality (PSE) was acquired. Via a bootstrap procedure, we acquired confidence intervals reflecting uncertainty of the fit. Table 1 represents 95% confidence intervals for individual observers and for the pooled data of all observers. Non-overlapping confidence intervals were taken as a significant difference between conditions. Statistical analysis was performed on the pooled data of all observers.

The surround had a significant effect on the perceived direction of motion in both surround conditions. In the monocular surround condition, the PSE for leftward surround motion was significantly smaller than the PSE for rightward surround motion (MS-l, 95% CI: -0.11:-0.06 vs. MS-r, 95% CI: 0.06:0.11). The same holds for the interocular surround condition: The PSE was significantly smaller for leftward than for rightward surround motion (MS-l, 95% CI: -0.08:-0.02 vs. MS-r, 95% CI: 0.00:0.05).

Next, we compared the difference in biases of rightward and leftward surrounds (Figure 4, lower panel) between the monocular and interocular surround conditions using a paired *t* test on the mean PSEs of the five observers. The surround bias is significantly larger for the monocular compared to the interocular condition, $T(4) = 2.8$, $p = .003$.

Discussion

This experiment was designed to investigate whether multiple levels of motion processing are involved in surround inhibition. In both surround conditions, the perceived direction of motion in the center was shifted in a direction opposite to that of the surround. This implies that the observed center-surround interactions are at least partly acting at a binocular level. When center and surround were presented to the same eye, this shift was larger compared to when the surround was presented to the other eye. This implies that center-surround interactions at monocular levels of processing also contribute.

Quantitatively, the surround modulation was about twice as large when center and surround were presented within one eye compared to when they were presented between both eyes. This suggests that monocular and binocular levels of processing contributed about equally to surround inhibition.

General discussion

In two experiments we studied surround interactions in visual motion processing. The first experiment revealed that dominance of a rival motion target varies with size and contrast of surround motion. More specifically, increasing the size of surround motion increased the dominance of the rival motion target when it moved in the opposite direction, whereas its dominance was decreased when it moved in the same direction. However, same direction motion had the largest effect on dominance. Varying luminance contrast of both center and surround had a less pronounced effect on dominance of the rival targets. Only for same direction motion, an effect of luminance contrast was observed: at the lowest contrast, dominance of the motion target first decreased, then increased when the size of the surround increased. In the second experiment we showed that the observed surround interactions are operating on both monocular and binocular levels of processing: Dichoptic presentation of center and surround lead to a significant shift of the perceived direction in the center. However, this shift was weaker than when center and surround were presented monocularly.

We set out these experiments to study surround interactions often observed in neurophysiology. Our results are in line with those of single-cell recordings. That is, surround interactions

- (1) are predominantly inhibitory.
- (2) vary as a function of size and contrast, and
- (3) involve multiple levels of processing.

Next, we discuss our findings and their relation to physiology in greater detail. Surround interactions observed in single-cell studies are often inhibitory, although surround facilitation is also observed. For example, Allman et al. (1985) found many neurons whose response was inhibited by presenting same-direction motion to the surround. Only few neurons have been

described showing surround facilitation (e.g., Allman et al., 1985; Tanaka et al., 1986). Psychophysical studies have primarily focused on center-surround inhibition as well (e.g., Tadin et al., 2003). To summarize our results and those of single-cell recordings, surround facilitation is observed, but surround inhibition is more prominent.

As discussed above, the magnitude of surround inhibition varies as a function of size and contrast. Tadin et al. (2003) recently showed that duration thresholds and magnitude of the motion aftereffect (MAE) (both assumed to be indicators of magnitude of surround inhibition) (see Anstis, Verstraten, & Mather, 1998) varied with stimulus size and contrast. While duration thresholds increased with increasing size and contrast of a motion stimulus, the magnitude of the MAE decreased. These findings were supported by a recent study of Pack et al. (2005), who recorded responses of neurons in MT of the macaque. For low-contrast motion, responses kept increasing with increasing size of the motion stimulus. In contrast, the response to high-contrast motion peaked at a certain stimulus size after which the response dropped. Our results are in line with these findings: Increasing the size of surround motion decreased dominance of a rival motion target. Increasing luminance contrast had a less pronounced effect in our study. Surround inhibition was about equal across several contrasts, although surround inhibition peaked at a smaller surround size at the lowest contrast.

Surround interactions in motion processing have been described in V1, MT, as well as in MST. Most of these studies have focused on area MT. Jones et al. (2001) recently showed that surround suppression in motion processing can also be observed in V1. Interestingly, from anatomical studies it is known that input to MT is largely binocular (Felleman & Kaas, 1984), whereas V1 is subdivided in ocular dominance columns, which receive monocular input (Wiesel, Hubel, & Lam, 1974). In our study, interocular (between-eye) presentation of center and surround produced a smaller shift in perceived direction of center motion than within-eye presentation. From this we can infer that the magnitude of surround inhibition was larger for within-eye presentation than for interocular presentation. Assuming that our within-eye surround condition involved both monocular and binocular levels and our between-eye condition only binocular levels, we infer that the within-eye surround effect is the result of surround interactions at binocular as well as monocular levels of processing. These monocular and binocular components might correlate with surround interactions observed in V1 and MT. A monocular contribution to surround interactions might be mediated by V1 or via feedback connections from MT to V1 (a suggestion put forward by Jones et al., 2001, and supported by Hupé et al., 1998). Although we can only speculate about the anatomical underpinnings of the observed center-surround interactions, we can conclude that they occur at monocular and binocular levels of processing.

Our experiments were mainly aimed at studying surround interactions, yet the results of Experiment 1 also add to accumulating evidence of contextual modulation during binocular rivalry (Levelt, 1965; Fukuda & Blake, 1992; Alais & Blake, 1998; Alais & Blake, 1999; So-

bel & Blake, 2002; Carter, Campbell, Liu, & Wallis, 2004; Paffen et al., 2004). Although the suggestion of surround interactions during binocular rivalry has been put forward in some of these studies, we have now tested this more directly, by looking at same direction inhibition and opposite direction facilitation separately.

The use of binocular rivalry also allows us to explore another aspect of surround interactions: Does surround inhibition have the same effect on center motion as decreasing the center's luminance contrast? For example, it has been reported that perceived contrast of center motion decreases when surrounded by same direction motion (Takeuchi & De Valois, 2000). Binocular rivalry can also provide insight into this question. According to Levelt (1965), manipulating the stimulus strength of one target engaged in binocular rivalry changes the time this target will be suppressed, leaving its mean dominance duration unaffected. For example, decreasing the stimulus contrast of one target leads to increased dominance of the other. In this respect, it is informative to look at how the surround motion influenced mean dominance durations of the center targets in Experiment 1. When surrounded by the same direction of motion, the mean dominance duration of the rival motion target decreased somewhat in some conditions. However, the increase in predominance of the rival static target was mainly caused by an increase in mean dominance duration of the static target (Figure 2, lower panels). Thus, adding surround motion mainly modulated the dominance duration of the static target. If we apply Levelt's (1965) concept of stimulus strength, adding a same-direction surround decreases stimulus strength of the rival motion target in a similar manner as decreasing this target's luminance contrast. This implies that surround interactions in motion processing act to modulate effective contrast of motion stimuli.

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Chapter 5

Center-surround inhibition deepens binocular rivalry suppression

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Abstract

When dissimilar stimuli are presented to each eye, perception alternates between both images – a phenomenon known as binocular rivalry. It has been shown that stimuli presented in proximity of rival targets modulate the time each target is perceptually dominant. For example, presenting motion to the region surrounding the rival targets decreases the predominance of the same-direction target. Here, using a stationary concentric grating rivaling with a drifting grating, we show that a drifting surround grating also increases the depth of binocular rivalry suppression, as measured by sensitivity to a speed discrimination probe on the rival grating. This was especially so when the surround moved in the same direction as the grating, and was slightly weaker for opposed directions. Suppression in both cases was deeper than in a no-surround control condition. We hypothesize that surround suppression often observed in area MT (V5) – a visual area implicated in visual motion perception – is responsible for this increase in suppression. In support of this hypothesis, monocular and binocular surrounds were both effective in increasing suppression depth, as were surrounds contralateral to the probed eye. Static and orthogonal motion surrounds failed to add to the depth of rivalry suppression. These results implicate a higher-level, fully binocular area whose surround inhibition provides an additional source of suppression which sums with rivalry suppression to effectively deepen suppression of an unseen rival target.

Introduction

When a dissimilar stimulus is presented to each eye, an observer's perception alternates between both images, a phenomenon known as binocular rivalry (Alais and Blake, 2005). Two aspects of this phenomenon have intrigued visual neuroscientists: the fact that the conflict is resolved by an alternation between the competing monocular images (rather than, for example, resulting in transparency, or a summation), and the fate of the unseen image, which is removed from consciousness despite being physically present on the retina. A thorough knowledge of both aspects of rivalry is necessary if the mechanisms underlying the phenomenon are to be understood. This paper focuses on the second issue, suppression depth.

Rivalry alternations are irregular and typically occur at a rate averaging about 0.5 – 1 Hz. A variety of spatial and temporal factors have been shown to influence the rate of rivalry alternations. Breese (1899) observed that the predominance of one image over another in rivalry was markedly enhanced as the luminance intensity of that image increased. Levelt (1965) showed that increasing the stimulus strength of the rival images produces an increase in alternation rate, where stimulus strength is defined in terms of luminance and contour density. Temporal factors can also influence rivalry. The incidence of rivalry between two motion stimuli becomes less likely as temporal frequency increases and the alternation rate increases (Carlson & He, 2000).

Top-down factors have also been shown to influence rivalry alternations. Lack (1978) showed in a series of experiments that naïve observers could voluntarily exert some control over rivalry alternation rate. This was especially so after a period of training, although, importantly, none of Lack's observers were able to completely stop rivalry alternations. Lack also ruled out a role for peripheral mechanisms in alternation rate, such as changing pupil size, accommodation, or blink rate and concluded that a central 'switching' mechanism controlled rivalry. Top-down influences have also been shown to exert an influence on the reversal rate of other forms of perceptual bistability (Strüber & Stadler, 1999).

Factors that alter rivalry rate and dominance duration are generally those that involve the parameters of the rival stimuli themselves (e.g., contrast, spatial frequency, etc.). There are, however, some top-down influences which provide interesting exceptions to this rule. One example comes from Kovacs et al (1996) who showed that coherent images mixed between the eyes were capable of becoming dominant as coherent whole images, presumably driven by a top-down Gestalt influence. This process of interocular grouping was first reported by Diaz-Caneja in 1928 (translation: Alais et al 2000). Alais and Blake (1998) investigated a similar issue of stimulus context. They observed that if two elements are engaged in rivalry (drifting gratings), but one forms part of a larger global stimulus (a globally coherent, multi-aperture motion stimulus), then that element was less likely to be suppressed by the single grating rivaling with it. It was proposed that higher-level areas involved in signaling global motion coherence exerted a modulatory feedback influence over the rivalry process at a lower level between the two local gratings, strengthening the signal of the grating belonging to the global stimulus.

In a previous paper (Paffen, te Pas, Kanai, van der Smagt & Verstraten, 2004), we investigated related surround effects. We introduced non-rival stimuli in the area surrounding the rival stimuli and demonstrated that stimulation in surround regions influenced dominance durations and alternation rates. In these experiments, rival gratings moved in opposite directions and one was surrounded by an annular grating whose direction was the same as one of the rival stimuli. This caused the predominance of the target with the same-direction surround to decrease. That is, the rival stimulus with an opposite-direction surround was more dominant than that with the same-direction surround. It was proposed that the increase in grating predominance when surrounded by opposed motion resulted from surround inhibition of the kind that has been observed in motion-selective neurons. Surround inhibition refers to the finding that the response of a neuron to its preferred direction of motion decreases when same direction motion is also presented to its non-classical receptive field (Allman, Miezin & McGuinness, 1985; Born & Tootell, 1992). Thus, a same-direction surround would decrease the stimulus strength of the surrounded rival grating, causing an increase in the predominance of the other grating.

In the present paper, we investigate whether surround motion can also affect the depth of suppression of a surrounded rival target. Depth of suppression refers to the fate of the suppressed stimulus. Despite a suppressed grating being completely absent phenomenally during binocular rivalry, measurements of the neural representation of that grating (as indicated by contrast sensitivity) indicate that it is only suppressed by roughly a factor of two relative to the dominant stimulus (Blake & Camisa, 1979; Makous & Sanders, 1981; Nguyen, Freeman & Wenderoth, 2001). Thus, although rivalry suppression may render a stimulus temporarily invisible, its cortical signal is attenuated rather than eliminated. In order to investigate this question experimentally, we dichoptically presented a horizontally moving grating and

a stationary concentric grating. The observer's task was to discriminate a brief speed pulse (an increase or a decrease) in the drifting grating, and sensitivity to the probe triggered during perceptual dominance and suppression is compared. The ratio of dominance-to-suppression thresholds provides a measure of the depth of rivalry suppression. On the basis of center-surround inhibition, we hypothesized that adding a same-direction surround to the motion grating would add an additional source of suppression, leading to a greater depth of suppression for that grating than would be observed without a surround.

General methods

Observers

Four observers performed in the experiments, authors CP and DA and two naïve observers. All had normal or corrected-to-normal vision.

Apparatus & Stimuli

Stimuli and conditions are presented in Figure 1. Stimuli were generated using Matlab and the Psychtoolbox (Brainard, 1997; Pelli, 1997) and displayed on a gamma-linearized LaCie Electron 22" monitor (75 Hz vertical refresh) connected to an Apple Macintosh G4 and viewed through a mirror stereoscope. Binocular fusion was aided by a white ring filling the gap between center and surround, and by a white square drawn around the annulus. There was also a central fixation point. The rival stimuli consisted of one horizontally moving vertical grating and a stationary concentric ring. The rival targets could each be surrounded by an annulus containing a horizontally moving grating. The grating in the annulus could move in the same or in the opposite direction as the central motion target.

All gratings had a spatial frequency of 1.96 cycles/deg. Motion stimuli had a speed of 1.27 deg/sec and were presented at 99% contrast. The mean luminance of both the gratings and the background was 33 cd/m². The diameter of the center targets was 1.24 deg; the surrounding annulus was 1.70 deg wide. There was a gap of 0.09 deg between the center aperture and the annulus.

Procedure

To measure depth of suppression, we compared the performance of observers on a discrimination task on the motion target while it was perceptually dominant versus when it was suppressed. Observers were instructed to judge whether a brief speed pulse presented to the motion target was an increment or decrement, according to a method described previously

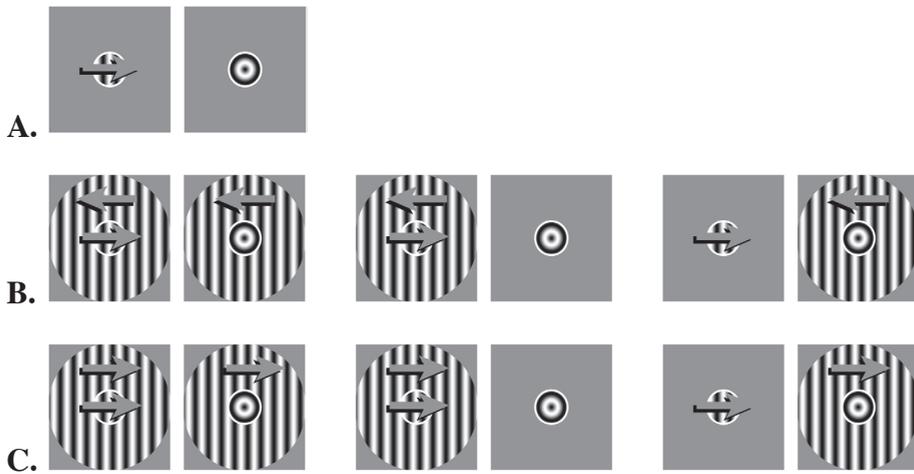


Figure 1. Stimuli and conditions used in Experiment 1. Pairs of stimuli were presented dichoptically, one stimulus to the left eye, and the second one to the other eye. A. The no surround condition, B and C the different surround conditions. B. The opposite direction conditions, C. The same direction conditions. For the surround conditions, the left column represents the binocular condition, the middle column the monocular condition, and the right column the interocular condition.

(Nguyen, Freeman & Alais, 2003). Briefly, the speed of the moving rival grating smoothly increased or decreased according to a raised Gaussian profile, after which it returned to its baseline speed. Because the speed change was multiplicative (speed was either multiplied or divided by the raised Gaussian), the proportionate speed change was the same for increments and decrements. To acquire 75% correct thresholds, the amplitude of the Gaussian speed pulse was varied from trial to trial using QUEST, an adaptive staircase method (Watson & Pelli, 1983) and observers had to indicate whether the speed change was an increment or decrement.

Upon initiating a trial, the rival targets appeared. In ‘dominance’ conditions, observers waited until the motion target was completely dominant and in ‘suppression’ conditions, observers waited until the stationary target was dominant. When a given target was dominant, observers pressed the space bar to trigger the brief speed pulse. 150 ms after pressing the space bar, the speed pulse appeared, which lasted for 120 ms in total and had a full bandwidth at half-height of 50 ms. 150 ms after returning to baseline speed, the trial was terminated and the observer indicated whether the speed pulse was an increment or decrement. If the dominant percept altered before or immediately upon pressing the space bar, the observer could repeat the trial. The repetition of an ‘erroneous’ trial ensured that pulse discrimination occurred in the respective ‘dominance’ or ‘suppression’ condition without exception. Each run

consisted of 32 trials, and observers completed at least 4 runs per condition. The direction of motion of the center target as well as whether the speed pulse was an increment or decrement was randomized from trial to trial.

Conditions

Our experiments examined the influence of surround motion on depth of rivalry suppression of the drifting rival target. There was a no-surround baseline condition (NS), in which the rival stimuli were presented alone (a drifting grating to one eye, a stationary target to the other), and a total of 6 surround conditions (see Figure 1):

- (1) binocular surround, same direction (BS)
- (2) monocular surround, same direction (MS)
- (3) interocular surround (i.e., monocular but other eye), same direction (IS)
- (4) binocular surround, opposite direction (BO)
- (5) monocular surround, opposite direction (MO)
- (6) interocular surround, opposite direction (IO)

Since each surround condition included a ‘dominance’ and a ‘suppression’ block, there were 14 conditions in total, including the baselines. Each condition was repeated at least 4 times per observer. The experiment was preceded by several practice blocks whose data was not analyzed. The total duration of the experiment was about 6 hours.

Experiment 1

With surround stimuli shown to alter the predominance of a central rival target (Paffen et al., 2004), Experiment 1 investigates whether a complementary effect of surround motion on the suppression depth of a rival target can be observed. If such an effect does exist, it will be demonstrated by greater suppression for the 6 surround conditions relative to the no-surround baseline condition. More specifically, the known physiological effects of center-surround inhibition indicate that same-direction surrounds should produce greater suppression in the central grating than would be observed with opposite direction surrounds.

Results

Figure 2a shows the mean speed discrimination thresholds for four observers measured during dominance and suppression for the no-surround baseline condition and the six surround conditions. For all conditions, thresholds measured during suppression were significantly higher than those measured during dominance. Even the condition yielding the smallest T -score (the no-surround condition) was highly significant with $T > 3.4$ and $p < 0.003$.

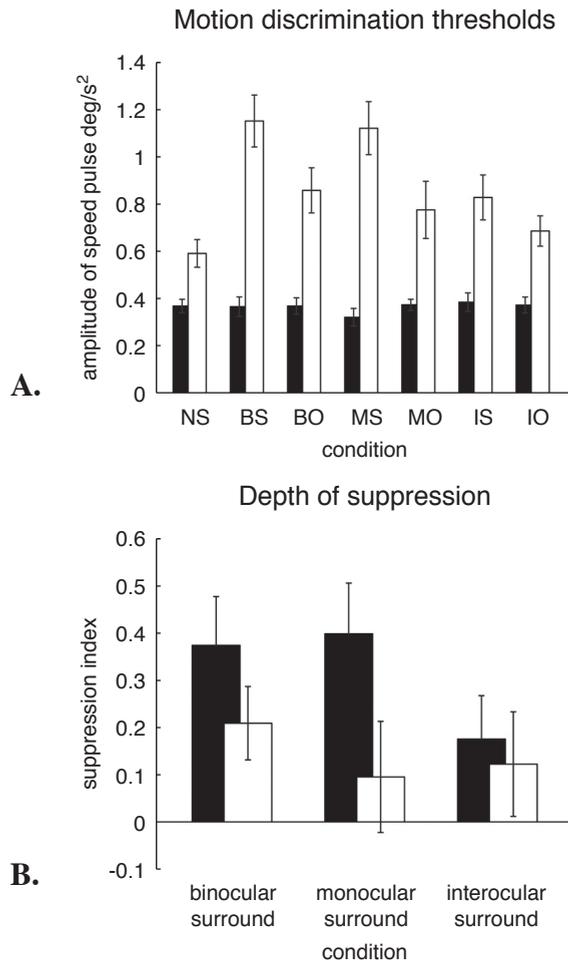


Figure 2. Results of Experiment 1. Error bars represent standard errors of the mean. Results are pooled for all four observers. A) Motion discrimination thresholds for dominance and suppression trials for all conditions in deg/s^2 (ns: no surround, bs: binocular same, bo: binocular opposite, ms: monocular same, mo: monocular opposite, is: interocular same, io: interocular opposite). Black bars represent thresholds for dominance trials, white bars represent thresholds for suppression trials. B) Depth of suppression. Following common practice, depth of suppression indices were calculated by dividing thresholds from dominance trials by thresholds from suppression trials. Next, the resulting ratio for the no-surround condition was subtracted from those of the surround condition, to show only the additional effect due to surround suppression. These indices of depth of suppression are plotted for the three different surrounds (binocular, monocular and interocular). The black bars represent indices for same direction surrounds, the white bars indices for the opposite direction surround.

To calculate the suppression depth associated with each of the surround conditions, we divided the dominance thresholds by the suppression thresholds to produce a suppression index. This index would have a value of 1.0 if there were no suppression, as thresholds in both dominance and suppression would be identical. Given that thresholds during suppression are all higher than those for dominance, the suppression indices will be all less than 1.0 by an amount that quantifies suppression depth. Before plotting these suppression indices, the suppression index for the no-surround condition was subtracted from those for the six surround conditions. Thus, the suppression indices shown in Figure 2b plot the additional contribution made to rivalry suppression due to the suppressive effect of the surround stimuli. Values greater than zero indicate that surround stimuli increase the depth of rivalry suppression of the central target. Overall, adding a surround significantly increased suppression: depth of suppression in surround conditions was significantly larger than in the no surround condition ($T = 5.4, p < 0.001$).

A two-way ANOVA was conducted on the suppression indices with the factors being the direction of motion of the surround (same vs. opposite) and the type of surround (binocular, monocular or interocular). This analysis revealed significant main effects of both factors: direction of surround motion ($F = 10.8; p = 0.01$) and surround type ($F = 5.7; p = 0.04$). No significant interaction between the factors was observed (motion*surround: $F = 1.8; p = 0.2$). As can be seen in Figure 2b, the significant main effect of surround motion arises because there is greater suppression depth when the surround moves in the same direction as the central rival target compared to when the surround moves in the opposite direction. The main effect of surround type indicates differential effects of a surround on suppression depth depending on whether it was a binocular, monocular or interocular surround. Binocular surrounds lead to the largest increase in suppression depth, interocular surround to the smallest increase. This order of effect sizes is supported by a linear regression across these conditions that showed a significant linear trend ($F = 10.3; p = 0.007$). However, post hoc pairwise testing revealed a significant difference only between the binocular and interocular surround conditions ($T = 2.7, p = 0.007$). Thus, although suppression depth increases linearly from interocular, via monocular to binocular surrounds, the increase between successive pairs is not significant.

Experiment 2

It might be argued that the increased suppression depth we observed with the six motion surrounds was mainly due to the fact that there was a surround present at all, independent of whether or not the surround contained motion. Also, the six surround conditions in Experiment 1 contained motions that were either iso-directional or anti-directional. For these reasons, we repeated our speed sensitivity measurements under three new conditions. Depth of suppression was measured using a surround moving orthogonally to the central rival target. In

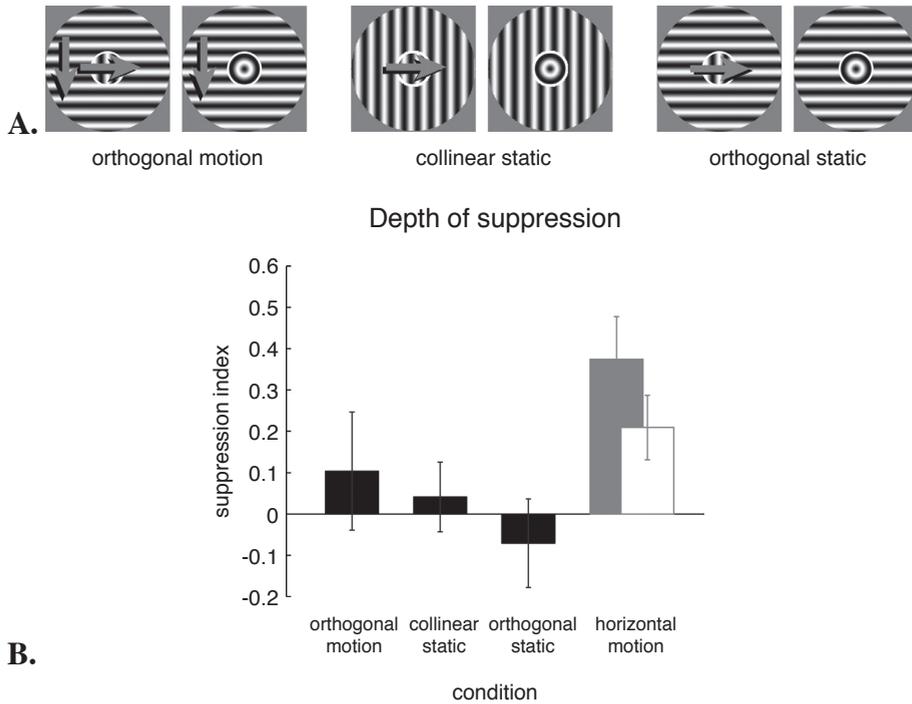


Figure 3. Stimuli and results of the control experiment. A) Stimuli: The center targets were the same as in Experiment 1. For all conditions, surrounds were presented to both eyes. In the orthogonal motion condition, a horizontal grating moved orthogonally to the motion target. In the collinear static condition, a static surround was presented with an orientation collinear to the motion center target. In the orthogonal static condition, the surround contained an orientation orthogonal to the center motion target. B) Results: The suppression depth indices were calculated in the same manner as for Experiment 1 so that only the additional suppression due to the surround stimulus is plotted. For all three surround conditions, the suppression depth indices are not significantly different from zero. For comparison, the results from Experiment 1 of the binocular same-direction and binocular opposite-direction surround conditions are plotted (the dimmed gray and white bars respectively). Error bars represent standard errors of the mean.

addition, two kinds of stationary surrounds were tested; one with an orientation collinear and one with an orientation orthogonal to the motion target. Figure 3a illustrates the three conditions. Since the results of Experiment 1 showed that binocular surrounds exert the greatest additional suppressive effect on the central rival target, the three conditions were run using only binocular surrounds. The rival targets and all methodological details were the same as used in Experiment 1. Three of the observers that performed in Experiment 1 also took part in this experiment.

Results

Speed sensitivity thresholds for the three surround conditions were measured during dominance and during suppression. The ratio of dominance to suppression thresholds was calculated to find suppression depth, and the suppression depth obtained from the no-surround baseline in Experiment 1 was subtracted in order to show the suppressive effect of the surround stimuli alone. The results (averaged across the 3 observers) are presented in Figure 3b. There are two key findings: (i) results from an ANOVA revealed that the difference between the three surround conditions is not significant ($F = 1.4$; $p = 0.3$), and (ii) none of the three conditions lead to a significant increase in suppression beyond the level obtained with the no-surround baseline (One-sample t-tests: $T < 0.7$ (largest T); $p > 0.24$ (smallest p)). Thus, stationary surrounds of either orientation do not affect depth of suppression and nor do translating surrounds if their direction is orthogonal to that of the rival motion target.

Discussion

We find that rivalry suppression is deepened by the presence of a drifting grating surrounding a rival motion stimulus. Thus, the attenuation of a suppressed image's signal, typically by about a factor of two (Blake & Camisa, 1979; Makous & Sanders, 1981; Nguyen et al., 2001), appears to be further attenuated by the presence of the surround motion. This is consistent with our predictions based on the surround inhibition hypothesis that adding surround motion around a rival motion grating would cause an additional suppressive influence that would sum with rivalry suppression to deepen the overall level of suppression. This result also extends an earlier finding that surround stimuli altered the predominance of a stimulus in rivalry (Paffen et al., 2004) in ways that were consistent with surround suppression.

The additional suppressive component to rivalry suppression produced by surround inhibition appears to be a rather general one since both same- and opposite direction surrounds effectively increased suppression depth compared to a no-surround baseline (see Figure 2a). This is consistent with data from single-unit recordings in area MT which show that the classical receptive fields of the vast majority of cells have large modulatory surround fields (Raiguel, van Hulle, Xiao, Marcar & Orban, 1995; Bradley & Andersen, 1998) whose activation almost always produces a suppression of the classical receptive field response (Allman et al., 1985; Xiao, Raiguel, Marcar, Koenderink & Orban, 1995; Bradley & Andersen, 1998). Another point worthy of note is that the various surrounds appeared to exert no significant influence on the rival grating during dominance, as thresholds for speed-pulse detection in Figure 2a are all very similar across the six surround conditions and are not significantly different from the dominance threshold recorded for the no-surround condition.

At first sight, the lack of a surround effect on dominance thresholds appears to be odd.

However, this result is not inconsistent with other investigations. For example, in Nguyen et al (2003), suppression depth deepened across a range of conditions but without any change at all in dominance thresholds. In other words, the suppression-deepening effect was determined solely by how deeply suppressed the ‘suppressed’ target was, and not by how ‘visible’ the dominant target was. Nguyen et al’s results are especially relevant since they also used discrimination of speed pulses as the task in their threshold measurements.

One of the predictions of the surround inhibition account is that same-direction surrounds should add more to the suppression of the rival target than would opposite direction surrounds. A number of studies have specifically compared same- and opposite-direction surrounds and found that opposite-direction surrounds were less suppressive of the response in the classical receptive field than were same-direction surrounds (Allman et al., 1985; Xiao et al., 1995; Bradley & Andersen, 1998). Indeed, a minority of cells actually exhibit response facilitation when stimulated by an opposite direction surround (Tanaka, Hikosaka, Saito, Yukie, Fukada & Iwai, 1986). Consistent with these observations, our suppression depth measurements revealed a significant main effect of surround direction (see Figure 2b), with same-direction surrounds adding more to rivalry suppression than opposite-direction surrounds.

In Experiment 2, we tested motion surrounds with an orthogonal direction relative to the central grating and found little or no addition to rivalry suppression. While most single-unit neurophysiological work on MT surrounds has focussed on preferred vs. antipreferred directions in the surround, relative disparity and relative speed (Allman et al., 1985; Bradley & Andersen, 1998; Raiguel et al., 1995; Xiao, Raiguel, Marcar & Orban, 1998), Tanaka et al. (1986) did measure the directional tuning curve of surround motion suppression. Their finding was that suppression was maximal for same direction surrounds and steadily declined as the angle between the center and surround motion increased. When the center and surround motion directions differed by 90 degrees, there was little or no suppression such that the response to an orthogonal surround was almost identical to the no-surround response. This pattern of results is in close agreement with our orthogonal-direction surround condition (see Figure 3b) in which little or no additional suppressive effect was observed relative to the no-surround condition.

The ocularity of the surround stimulus was also important in mediating the size of the suppressive surround effect. We found that binocular surrounds were more effective than monocular, which were more effective than interocular surrounds (see Figure 2b). Presumably binocular surrounds are most effective because binocular summation in the neural surround field would strengthen the surround signal and thereby cause a greater degree of suppression on the units responding to the drifting grating rival target. Consequently, a binocular surround should result in a greater addition to the baseline suppression depth than would a monocular surround, as we observed. Monocular surrounds, however, are still quite effective, but less so if presented interocularly to the other eye.

Presentation of static surrounds appears not to exert a suppressive effect on rival motion targets (see Figure 3b). This is probably explained by the fact that mechanisms in distinct cortical areas are involved in the detection of static and drifting stimuli, most likely V1 and MT respectively, which would probably preclude center-surround interactions. Units in area MT, for example, where neurons are highly specialized for the detection of movement, respond only weakly and transiently to static stimuli. Because of this, there would be little or no scope for a suppressive interaction from the static surround on the classical receptive field in MT responding to the motion of the central rival target.

The present experiments can be compared with those of Alais and Blake (1999). In their experiments, facilitative rather than inhibitory effects were reported when a static grating was flanked by another static grating, especially when the gratings were collinear and adjacent. The two paradigms are similar in that adding a flanking grating is not unlike adding a (partial) surround grating. However, there are important differences between the paradigms. First, in Alais and Blake (1999), the two gratings were horizontally separated by several degrees, making it doubtful that one grating was even within the spatial zone of the other grating's surround field. Second, even if it were, the point remains that the small flanking grating would provide only a partial stimulus for the much larger surround field. These differences may be important, because the pattern of data obtained in Alais and Blake's experiments were also completely different to ours, being primarily facilitative rather than inhibitory. Together, this points to a different substrate underlying the two data sets, and the most likely account of Alais and Blake's data is in terms of lateral intrinsic connections in V1. Supporting this, the level of facilitation they observed dropped when the gratings were oriented in parallel, and dropped again if they were orthogonal, exactly as predicted from patterns of intrinsic connectivity. Thus, the important differences between their flanking experiments and our surround experiments suggest different neural substrates rather than a conflict of data.

In summary, the experiments described above show that a drifting surround stimulus can exert a strong effect on binocular rivalry by deepening the suppression of the surrounded (translating) rival target. Two factors that are important in this effect are the direction of motion of the surround relative to the central stimulus and the ocularity of the surround. First, same-direction surrounds add more to suppression depth than do opposite-direction surrounds, with no effect for orthogonal-direction surrounds. Second, binocular surrounds cause more suppression than monocular and interocular surrounds respectively. Surrounds that are static or that move orthogonally to the rival target appear not to exert a suppressive effect. We propose these findings are best explained in terms of surround inhibition that has been observed in motion-selective cells in monkey area MT (Allman, Miezin & McGuinness, 1985; Born & Tootell, 1992). Specifically, surround inhibition provides an additional source of suppression which sums with rivalry suppression to effectively deepen the suppression of the unseen rival target.

Acknowledgements

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Chapter 6

Attention speeds binocular rivalry

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Paffen, C.L.E., Alais, D., & Verstraten, F.A.J. Attention speeds binocular rivalry.

Abstract

During binocular rivalry, incompatible images presented dichoptically compete for perceptual dominance. It has long been debated whether binocular rivalry can be controlled by attention. Some studies report that attentionally selecting one of the rivaling images will increase its dominance, although the effect is generally weak. In this study, we seek to remove attention from the rivalry process by diverting attention to a demanding secondary task. The main finding is that diverting attentional resources from rival stimuli slowed the rivalry alternation rate, and did so in proportion to distractor-task difficulty. Since it is well known that reducing contrast also retards rivalry alternations, we repeated our experiment at several contrast levels and found that the retarding effect of diverting attention was equivalent in magnitude to halving stimulus contrast. Even very demanding distractors, however, did not arrest rivalrous alternations completely. We conclude that attention is not necessary for rivalry to occur, but that it plays a role in expediting rivalry dynamics. This effect is most likely due to attention increasing the effective contrast of the stimuli by boosting the gain of the cortical response. As a result, attending to binocular rivalry will speed up the alternation rate. The findings provide an explanation for the limited attentional control over binocular rivalry reported previously: the ability to lengthen dominance of a rival target by attention is limited due to the bottom up effect of attention, which increases the likelihood that a target will lapse into suppression.

Introduction

When each eye is presented with images that cannot be binocularly fused, perception becomes unstable and alternates stochastically between the two monocular images. This phenomenon is known as binocular rivalry (e.g. Blake & Logothetis, 2002; Alais & Blake, 2005). Since rivalry gained scientific interest, it has been debated whether rivalry involves competition at early or late stages of visual processing (Hering, 1964; Helmholtz, 1910/1962; Blake, 1989; Logothetis, 1998). According to a low-level view (Levelt, 1965; Blake, 1989), binocular rivalry is governed by typical low-level processes. For example, Levelt (1965) showed that the dynamics of binocular rivalry were influenced by stimulus contrast: lowering contrast slows the rate of rivalry alternations. Building on this concept of ‘stimulus strength’ and on other findings indicative of low-level influences on rivalry, Blake (1989) formalized a theory (now known as ‘eye rivalry’) that proposed a low-level site giving rise to rivalry involving inhibitory connections between monocular processing channels, presumably in primary visual cortex (V1). Support for this theory comes from neuro-imaging studies showing clear evidence that rivalry is caused by competition in V1 (Polonsky, Blake, Braun & Heeger, 2000), even in the representation of the blind spot in V1 where input is exclusively monocular (Tong & Engel, 2001).

More recently, evidence has emerged which favors a high-level site of binocular rivalry. The ‘stimulus rivalry’ theory posits that competition occurs at a higher level between stimulus representations that rival for conscious expression (Logothetis, 1998). In a critical psychophysical experiment, Logothetis, Leopold and Sheinberg (1996) swapped two orthogonal gratings rapidly between the eyes. Because the eye-swapping rate was several times faster than typical rivalry alternations, ‘eye rivalry’ predicted that several orientation flips should have been visible during a single period of eye dominance. Instead, Logothetis and his colleagues observed stable percepts lasting several swap cycles in which only a single grating was perceived. Other reports showed that Gestalt-like organization principles can provoke

grouping interocularly (Alais, O'Shea, Mesana-Alais & Wilson, 2000; Kovacs, Papatomas, Yang & Feher, 1996), implying a binocular locus for rivalry beyond the monocular levels proposed by eye rivalry.

In an attempt to account for findings supporting either the low- or the high-level view, several authors recently proposed that binocular rivalry is the result of competition at a multitude of visual processing stages. For example, Nguyen, Freeman and Alais (2003) reported that depth of rivalrous suppression (e.g. detecting a probe in a suppressed target) was dependent on stimulus complexity. Also, Wilson (2003) proposed a neural model that can account for results favouring both stimulus- and eye-based rivalry.

Regardless of theoretical perspective, one commonality in all binocular rivalry studies is that observers must report on some aspect of the rivalry process. For example, observers might continuously monitor rivalry alternations, indicate dominance durations, periods of piecemeal rivalry, or even report on brief probe stimuli so the that suppression depth can be measured (e.g. Fox & Check, 1968). Whatever the task, a conscious effort is required to complete it and attention is therefore allocated to the rival images. Since attention can be thought of as a process of selection from among competing objects and stimuli (Desimone & Duncan, 1995), one hypothesis would be that diverting attentional resources to a demanding secondary task might prevent rivalry alternations from occurring. That is, if rivalry dominance were simply a manifestation of a process of attentional selection, then diverting attention might lead to stabilized perception. A competing hypothesis would be that rivalry results fundamentally from the inability of the visual system to achieve binocular fusion and is a default outcome that proceeds automatically when fusion fails. According to this point of view, the perceptual alternations experienced during binocular rivalry have a low-level origin, and might therefore occur preattentively.

Some studies have examined the role of attention in binocular rivalry, most of which have focused on the effect of attentionally selecting one of the two rival stimuli. This generally lengthens the dominance period of the selected image, although relatively modestly (Lack, 1978; Meng & Tong, 2004). According to Helmholtz (1962) it was possible to keep a target dominant by selectively attending to it. This proposition was studied by Lack (1978), showing that – after some training – observers were indeed able to keep a specific target dominant by attending. However, as both Helmholtz (1962) and Lack (1978) put forward, it was only possible to control rivalry up to a certain degree; eventually, the attended target would lapse into suppression. More recent evidence also confirms that attention lengthens dominance periods but fails to prevent rivalry alternations entirely (Ooi & He, 1999; Meng & Tong, 2004).

In this study, rather than using attention to select one of the rival stimuli, we adopted an alternative approach. We had observers divert their attention from the rival stimuli and allocate it to a demanding distractor task surrounding the rival targets. Our interest was to

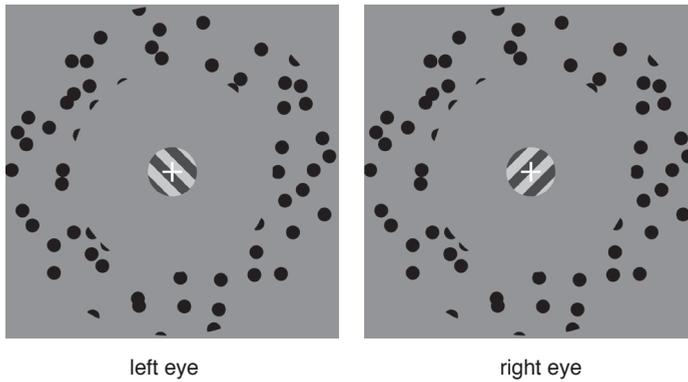


Figure 1. Basic depiction of the stimuli used in the experiments. Central rival targets instigated binocular rivalry. Dots in the surround moved in random directions. At random moments, a subset of the dots moved briefly in a horizontal direction.

examine how the dynamics of the rivalry process are affected by the allocation of attention. Specifically, by varying distractor-task difficulty, we quantify how the rivalry process functions under high and low levels of allocated attention, and by comparing across a number of contrast levels, we are able to equate the influence of attention on rivalry alternations as an effective change in stimulus strength.

Methods

Observers

Four observers (two of which were naïve to the purpose of the experiments) performed in the experiments. Observers CP and DA are authors of this paper. Observers had normal, or corrected to normal vision.

Stimuli

Stimuli are presented in Figure 1. Rival targets were square-wave orthogonal gratings (oriented -45 and 45 deg from vertical) with a spatial frequency of 2.1 cpd and were 0.6 deg in radius. The targets were each surrounded by an annulus containing black dots moving in random directions. The annulus was 1.6 deg in diameter; a gap of 1.8 deg separated center targets and annuli. Individual dots originated at a random position within the annulus, and made 7 steps in a random direction with a stepsize of 0.04 deg, resulting in a speed of 1.6 deg/s. The radius of individual dots was 0.2 deg. Dots and rival targets were presented on a

grey background with a luminance of 38 cd/m². In experiment 1, contrast of the rival gratings was 47.4% (Michelson), in experiment 2, contrast of the gratings was either 11.8, 23.7, 47.4 or 94.7%.

Procedure

Rival targets and surrounds were presented for 2 minutes. During 2-minute presentation, 20 visual cues were presented within rival targets and annuli for 0.2 s. Preceding half of the cues, a proportion of the random dots moved coherently along a single trajectory. This low coherent motion was presented for 0.5 s. In attention conditions, observers were instructed to indicate whether a cue was preceded by a burst of coherent motion. In experiment 1, observers performed in three rivalry conditions (passive, attend-difficult, attend-easy). In the passive condition, the coherence level was the same as in the attend-difficult condition. In this condition, observers did not perform the motion detection task. Coherence levels (attend-difficult and attend-easy) were chosen per observers after piloting and were 15 and 30% for CP and DA, and 25 and 35% for AP and JC, respectively. In pseudo-rivalry conditions, rivalry was mimicked by alternating the two orientations of the rival targets. A transition from one dominant percept to the other was mimicked by decreasing the contrast of target A to zero, while at the same time increasing the contrast of target B from zero to the baseline contrast level. Contrast increments and decrements occurred along half of a temporal Gauss and took 0.5 s to complete. In experiment 2, observers performed in 8 conditions (four contrast levels of the rival targets, passive and active viewing). Task and stimuli were similar to those in experiment 1. The coherence-level in experiment 2 was the same as for the attend-difficult condition in experiment 1.

Results

Figure 2a shows the mean alternation rate for passive viewing and for two levels of motion coherence in the motion detection task. As can be seen, performing the detection task slowed down the speed of alternations (passive > attend easy, $T(15) = 5.6$, $p < 0.001$). Moreover, if the task was difficult (low coherence, low d' (Figure 2b)), reversal rate was slower than when the task was easy (high coherence, high d' (Figure 2b)) (attend easy > attend difficult, $T(15) = 2.6$, $p = 0.008$). Since it might be argued that attending to a secondary task degrades the ability to track rivalry, we had the same observers track pseudo-rivalry (see Method section), while performing the motion detection task. Figure 2c shows that observers were very accurate at tracking pseudo-rivalry reversals while at the same time performing the detection task. In addition, performance on the detection task during pseudo-rivalry was similar to performance during real binocular rivalry (Figure 2b).

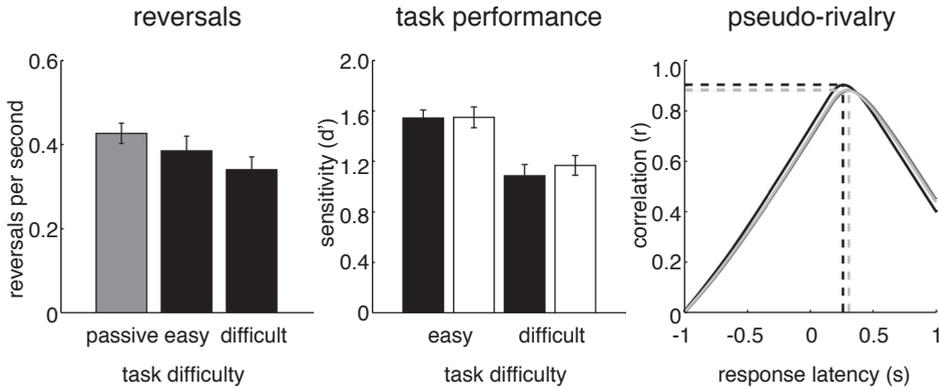


Figure 2. Results of Experiment 1. Left panel: Mean alternation rate for the passive, attend-easy and attend-difficult conditions. Middle panel: Sensitivity (d') for performing the attention task for the attend-easy and attend-difficult conditions, for real rivalry (black bars) and pseudo-rivalry (white bars). Error bars represent standard errors of the mean. Right panel: Temporal correlations between a physical pseudo-rivalry switch and the observers' response to the switch. The solid black, light-grey and dark-grey lines represent the correlations for the passive, attend-easy, and attend-difficult conditions respectively. The dashed lines depict the maximum correlations for each of the three conditions.

Since Levelt (1965), it is known that lowering the contrast of rival targets slows down rivalry alternations. In experiment 2, we capitalized on this finding and compared alternation rate for rival targets presented at different contrasts for passive viewing and during performance in the motion detection task. This approach allowed us to quantify the contribution of attention to rivalry dynamics. Figure 2a shows that the effect of attention was about constant across different target contrasts. Interestingly, as shown in Figure 2a, performing the detection task had a similar effect on rivalry alternations as halving the target's contrast in passive viewing; alternation rate for passive viewing at 50% contrast is similar to alternation rate while performing the detection task at 100% contrast. The effect of attention was not caused by different sensitivity to the motion detection task, that is, d' for the task was not significantly different across different contrast levels (Figure 3b). Although the magnitude of attentional modulation is likely to be dependent on the difficulty of the task, the results underline that reducing contrast and diverting attention have similar effects on rivalry alternations.

Discussion

In two experiments, we have shown that disengaging attention from rivalry slows the speed of rivalry alternations. Moreover, when engaged in a difficult secondary task, rivalry was slowed more than when doing an easy task. Thus, the more attentional resources were taken

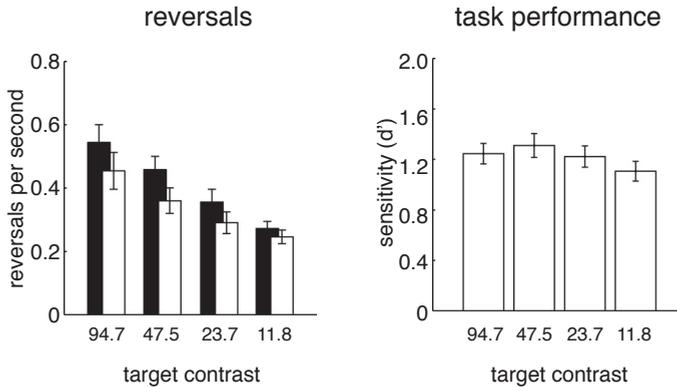


Figure 3. Results of Experiment 2. Left panel: The bars represent mean reversal rates across different targets for passive viewing (black bars) and diverted attention (white bars). Left panel: Sensitivity (d') for performing the attention task across different target contrasts. Error bars represent standard errors of the mean.

away from tracking rivalry, the slower alternations became. This drop in alternation rate was not due to a degraded ability to track rivalry alternations due to the secondary task; observers were highly able to track pseudo-rivalry mimicking real rivalry alternations while performing the attention demanding task. In addition, we show that attention acted in a contrast-like manner; performing the secondary task had a similar effect on rivalry alternations as lowering the targets contrast.

The results provide an account for the limited attentional control over rivalry observed in the past. While some studies have shown that it is possible to lengthen dominance by directed attention (Lack, 1978; Meng & Tong, 2004; van Ee, van Dam & Brouwer, 2005), our results suggest that the limitation in keeping a target dominant is due to a lower-level effect of attention, which modulates target strength. We suggest that attention affects the strength of rival targets in a manner similar to changing the contrast of the targets. This proposition is supported by recent studies linking visual attention to the dynamics of neural responses. For example, Reynolds, Pasternak and Desimone (2000) observed attention-induced increases in contrast sensitivity in V4 neurons. These findings suggest that attention increases the strength of behaviorally relevant stimuli in manner similar to increasing the contrast of the stimuli (Reynolds, Pasternak & Desimone, 2000; Reynolds, 2004). As our manipulation of attention closely matches the effect of manipulating contrast (which also slows rivalry alternations), we propose that disattending from rivalry alters the neural response to the rival targets in a manner similar to decreasing the contrast. As a result, alternation rate is slowed.

Also of interest is a recent finding by Blake, Sobel & Gilroy (2003), who showed that when rival targets move across the visual field, rivalry is slowed. They hypothesized that local

adaptation is a crucial factor in rivalry dynamics. Since contrast affects local adaptation (e.g. Hammond, Mouat & Smith, 1985), it appears that the results reported here are in agreement with those of Blake, Sobel and Gilroy (2003): when the strength of rival targets is lowered, either by lowering local adaptation, contrast, or diverting attention, rivalry is slowed.

In summary, our results show that attention is crucial in rivalry dynamics; attending to rivalry boosts rivalry alternations. Our findings also provide an account for the limited control over binocular rivalry observed previously. Although voluntary attention might increase dominance of a given target, low-level attention acts as to modulate target strength, thereby limiting attentional control.

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Summary & Conclusions

Visual perception of a stimulus is often affected by the visual context by which the stimulus is surrounded. For example, finding a blue pencil among blue pens is more difficult than finding this pencil among red pens. Clearly, the difficulty in finding the pen is caused by its visual context. Also, a visual context can change the appearance of a stimulus. Take for example the grey ring presented in Figure 1 of Chapter 1. When cut in half, the left half of the ring appears to be darker than the right half, although their grey value is physically the same. Both examples show that visual perception of a stimulus can be affected by its visual context. Much knowledge about how visual context influences visual processing stems from neurophysiological studies in non-human species. In this dissertation, this knowledge from neurophysiology is used to study the following question: how is visual perception influenced by visual context?

Chapter 1

From neurophysiological studies in different species, much is known about how visual context affects visual processing at the neuronal level. For example, neurons in the visual cortex often respond to a specific stimulus feature presented to a specific part of the visual field. This area has been labeled the classical receptive field. However, the response to stimuli presented to the classical receptive field can be modulated by presenting stimuli outside this area. Such neurons show a center-surround organization. Stimuli presented to the surround of a receptive field often inhibit the response to the center; the response to the center will decrease. Less often, the response of neurons is facilitated by surrounding stimuli, in which case the response to the center will increase.

In this dissertation, binocular rivalry is used to study the influence of visual context on visual perception. Binocular rivalry occurs when each of the two eyes is presented with a different stimulus (a different target). Presenting stimuli in this way leads to an intriguing phenomenon in visual perception: perception will alternate in time between the target presented to the left eye and that presented to the right eye (see Figure 2 of Chapter 1). Binocular rivalry has proven to be a useful tool to study perceptual consequences of changes in aspects of visual stimuli. For example, changing characteristics of the rival targets will affect the time each target is temporarily perceived. As a rule, a ‘stronger’ target (for example,

due to higher contrast) will be perceived longer than its rival. This target is said to be more dominant. It is hypothesized that, if visual context affects some aspect of visual processing, it is likely that we can observe the perceptual manifestation of this change in processing during binocular rivalry.

Chapter 2

This chapter deals with the following question: how is binocular rivalry between targets containing motion affected by surround motion? In order to find out, two targets containing opposite directions of motion were surrounded by an annulus containing motion in the same direction as one of the two targets. The results show that adding the motion surround increased the dominance of the target containing motion in the opposite direction to that of the surround. It is argued that the increased dominance of the opposite-direction target is the result of center-surround interactions as discussed above. The strength of the rival target with the same direction of motion as the surround was decreased due to center-surround inhibition. As a result, the opposite-direction target became more dominant.

Chapter 3

Is the influence of visual context on binocular rivalry as reported in Chapter 2 specific to motion? Neurophysiological studies show that center-surround interactions occur for neurons responding to both visual motion and orientation. In Chapter 3, we study how surrounds defined by motion, orientation and color modulate binocular rivalry. In addition, the influence of stimulus-contrast on contextual modulation of binocular rivalry is discussed. Recent studies have shown that center-surround interactions are dependent on contrast. Hunter, Pack and Born (2005) for example, described neurons manifesting surround inhibition at high contrast, and surround facilitation at low contrast.

The stimuli we used were: (1) orthogonally oriented targets, both surrounded by an annulus containing the same orientation as one of the two, (2) motion targets containing opposite motion directions, both surrounded by the same direction of motion as one of the two, and (3) isoluminant red and green targets, both surrounded by the same color as one of the two. Adding the surround modulated dominance of the center rival targets: at high contrast, a target with the same orientation as the surround was less dominant than a target with an orthogonal orientation. Also, a green target was less dominant than a red target when surrounded by a green annulus. For targets defined by motion, we replicated the results of chapter 2. Our contrast-manipulations lead to interesting results: for orientated targets presented at low contrast, the target with the same orientation as the surround was more dominant than the orthogonal orientation. The same was true for targets defined by motion: at low contrast, the

target with motion in the same direction as the surround was more dominant than the target with the opposite direction of motion. For low-contrast targets defined by color, adding the context did not lead to a significant difference between dominance of both targets. These results resemble those of neurophysiological studies, where center-surround interactions have been reported for stimulus-characteristics such as motion, orientation and color. In addition, the contrast-dependency of the influence of visual context on binocular rivalry observed in our experiments has also been observed in physiology. At high contrast, inhibition is most prominent, at low contrast, facilitation is observed.

Chapter 4

What is the effect of changing the size of a visual context on binocular rivalry? In the first experiment of Chapter 4, the size of an annulus containing motion surrounding a motion and a stationary target was varied. The surround contained motion either in the same or in the opposite direction to the motion target. In addition, the contrast of both targets and surrounds was varied. The results show that the size of the surround had a strong effect on dominance of the rival targets. Increasing the size of same-direction motion *increased* dominance of the stationary target. On the other hand, increasing the size of opposite-direction motion *decreased* dominance of the stationary target. Also, same-direction motion had a stronger effect on the dominance of the rival targets than opposite-direction motion.

Close inspection of dominance durations revealed that adding surround motion mainly affected dominance durations of the stationary target; dominance durations of the motion target were less affected. The relation between changing an aspect of the rival targets and dominance durations alludes to an observation made by Levelt (1965). Levelt's second proposition states that changing the strength of target A will affect the dominance of target B. Thus, lowering the contrast of target A will increase the dominance duration of target B, leaving that of target A unaffected. Since adding same-direction motion increased dominance durations of the stationary target (leaving dominance of the motion target relatively unaffected), it appears as though the motion surround was changing stimulus strength of the motion target in a manner similar to lowering the motion target's contrast.

In another experiment, we asked at what levels of visual processing center-surround interactions act. Center-surround interactions in motion processing have mainly been described at the level of middle temporal cortex (MT). This area mainly receives information from both eyes, implying that motion processing at this level is largely binocular. However, recent neurophysiological studies reported center-surround interactions in motion processing at the level of the primary visual cortex (V1). Visual processing at this level is to some extent monocular, where information from the left eye is processed separately from information originating from the right eye.

In this experiment, binocular rivalry was not used. Instead, the motion target was briefly presented to one eye. This target contained ambiguous motion in opposite directions. In addition, a motion surround was presented to one eye as well. This surround was either presented to the same eye as the motion target, or to the other eye. Without a motion surround, perception of the center motion was ambiguous (there was no systematic bias in perceiving leftward or rightward motion). Both types of motion surrounds made the center motion appear to be in the direction opposite to the surround. Again, this is indicative of center-surround interactions affecting visual perception of motion. The fact that between-eye presentation of center and surround biased perceived direction of the center motion implies that center-surround interactions at a binocular level of processing are active. However, within-eye presentation of center and surround lead to a larger shift in perceived direction than between-eye presentation. This suggests that center-surround interactions at monocular levels are also involved in visual motion processing.

Chapter 5

Previous chapters established that visual context affects dominance durations of rival targets. In chapter 5 the influence of visual surround on another aspect of binocular rivalry was studied. According to an influential theory on binocular rivalry by Blake (1989), alternation in perceptual dominance during binocular rivalry is the result of inhibitory interactions between neurons at the level of primary visual cortex. In this visual processing area, input from each eye is largely processed in separate layers. These two pools of neurons continuously inhibit each other. If the left-eye pool is (temporarily) inhibited more by the right-eye pool, the target presented to the right eye will be perceived. The amount by which one eye's pool is inhibited by the other eye's pool can be quantified by presenting a probe on the suppressed target. This amount of suppression is often labeled *depth of suppression*.

In an experiment measuring suppression depth, observers tracked binocular rivalry between a motion and a stationary target. When an observer indicated that the static target was perceptually dominant, a speed pulse was presented to the motion target. Observers were asked to discriminate between increments and decrements in speed of the (suppressed) motion target. In order to achieve the same specific performance level, a stronger pulse was required when the targets were surrounded by motion compared to when they were not. Moreover, a stronger speed pulse was required when the targets were surrounded by same-direction motion compared to when surrounded by opposite-direction motion. Thus, not only can a visual context modulate dominance durations of rival targets, it can also affect how much a rival target is suppressed. In addition, a same-direction surround suppressed a motion target more, suggesting that surround inhibition can deepen depth of rivalrous suppression.

Chapter 6

At this point, it is established that the perception of visual stimuli during binocular rivalry can be affected by visual context. However, stimuli presented outside central fixation can vary in behavioral relevance. More generally speaking, multiple visual objects often compete for visual attention. For example, we are often engaged in tasks where multiple objects require attention (for example while driving a car). In this chapter it is asked how visual perception is affected by performing a task on stimuli presented in the visual context. More specifically, it is asked how performing a task in the visual context modulates dominance durations of targets engaged in binocular rivalry.

Observers performed in an attention-demanding task, while at the same time continuously tracking rivalry alternations. The attention task consisted of detecting brief presentations of weak horizontal motion in otherwise incoherently moving dots in a ring surrounding the rival targets. Dominance durations of the rival targets increased when observers performed in the attention task compared to when they did not. In addition, dominance duration increased more if the task was difficult compared to when it was easy. This means that increasing the difficulty of the task decreased the speed of rivalry alternations.

In a second experiment, we studied the effect of performing the attention task at different levels of contrast of the rival targets. Contrast is known to affect dominance durations; decreasing contrast of rival targets increases dominance durations. Our results are in line with this observation, lowering contrast of the rival targets increased their dominance duration. Interestingly, performing the attention task increased dominance durations even more. The effect of performing the attention task was about constant at different contrast levels of the rival targets. Furthermore, performing the attention task had a similar effect on rivalry alternations as decreasing the contrast of the targets. Thus, dominance durations at 100 % contrast while performing the attention task were similar to dominance durations at 50 % contrast *without* performing the attention task. The latter observations dovetails with recent studies arguing that visual attention affects visual processing of a stimulus in a manner similar to lowering the contrast of that stimulus.

Conclusions

Based on the experiments discussed in this dissertation, several conclusions can be made: First, visual context can modulate visual perception during binocular rivalry. Second, the manner by which visual context can modulate binocular rivalry closely resembles the manner by which visual context affects visual processing at the neural level. Third, the influence of a visual context on binocular rivalry is dependent on the amount of visual attention involved in performing a task in the visual surround.

Several experiments described in this dissertation show that binocular rivalry can be affected by visual context. Visual context can both modulate dominance durations of rival targets and can affect the amount by which rival targets are suppressed.

Visual context affected binocular rivalry in a manner closely in agreement with observations from neurophysiology. At high contrast, dominance of a rival target sharing its defining feature with the surround was lowered. At low contrast, a surround boosted the dominance of a target with the same defining feature. This finding corresponds with adaptive center-surround interactions observed at the neuronal level. In addition, these adaptive center-surround interactions are likely to be a general property of visual processing since they were observed for stimuli defined by motion, orientation and color. Moreover, it was shown that surround interactions in motion processing occur at a multitude of visual processing stages.

The results also provide possible insights into the following question: how does the visual system efficiently code visual information under a variety of viewing conditions? The surround interactions described in this dissertation provide a possible solution to this problem. When contrast is low, the neural signal is amplified, when contrast is high, this signal is lowered. This adaptive interaction between context and local visual information might enable us to perceive the visual world efficiently under a variety of visibility conditions. A similar argument can be made for the role of visual attention. While inspecting the visual world, we often wish to attend to multiple objects. Our experiments suggest that the signal for a stimulus increases if more attentional resources are available.

The results of the last chapter show that the influence of visual context on visual perception is dependent on visual attention. Dominance durations of rival targets increased when performing a task on stimuli presented in the surround. Performing this task in the surround had a similar effect on dominance durations as lowering the contrast of the targets. Again, this result is in accordance with results from neurophysiology: the way the neural response to a visual stimulus is affected by attention is similar to the effect of changing the contrast of the stimulus.

The results in this dissertation also provide insights into the phenomenon of binocular rivalry. Binocular rivalry is evidently not independent of stimuli presented in the proximity of the rival targets. In addition, the results provide new insights into the relation between binocular rivalry and visual attention. Dominance durations during binocular rivalry are dependent on the amount of visual attention available for tracking binocular rivalry; diverting attention lengthens dominance durations. The results also provide an account for the limited control over binocular rivalry reported in the past. While trying to hold a target dominant by attention, the ability to do so is limited by a lower-level effect of attention, which speeds rivalry alternations.

In conclusion, this dissertation provides evidence that visual context can modulate visual perception in a manner similar to how visual context affects visual processing at the neural

level. Although it is generally not possible to study the influence of visual context at the level of individual neurons in humans, the results reported in this dissertation point towards a similar neural organization underlying contextual modulation of visual processing in humans as that observed in non-human species.

Samenvatting

In veel situaties in het dagelijks leven wordt de visuele waarneming van een object beïnvloed door de visuele context waarin het object wordt aangeboden. Het vinden van een blauwe vulpen tussen blauwe balpennen is bijvoorbeeld moeilijker dan het vinden van dezelfde pen tussen rode balpennen. De tijd die het duurt om de pen te vinden hangt in dit geval af van de gelijkentis tussen de vulpen en de andere pennen. Ook kan visuele context het waargenomen uiterlijk van een stimulus beïnvloeden. In figuur 1A van hoofdstuk 1 lijkt de linkerhelft van de doorgeknijpte ring bijvoorbeeld donkerder dan de rechterhelft. De grijstinten van de linker- en rechterhelft van de ring zijn echter fysiek hetzelfde; de achtergrond zorgt ervoor dat ze allebei verschillend lijken. Beide voorbeelden tonen aan dat visuele waarneming van een stimulus beïnvloed wordt door de visuele omgeving van de stimulus. Veel kennis over hoe visuele context visuele verwerking beïnvloedt is afkomstig van dierexperimenteel onderzoek. In dit proefschrift wordt deze kennis gebruikt bij het onderzoeken van de volgende vraag: hoe beïnvloedt visuele context visuele waarneming bij de mens?

Hoofdstuk 1

Het uitgangspunt bij het opstellen van hypothesen over de invloed van visuele context op visuele waarneming is kennis afkomstig van dierexperimenteel onderzoek. Neuronen in de visuele cortex (het gebied in de hersenen dat betrokken is bij visuele waarneming) reageren vaak op een specifieke eigenschap van een stimulus. Een bepaald neuron zal bijvoorbeeld reageren op een streep met een horizontale oriëntatie, maar niet op een streep met een verticale oriëntatie. Ook reageren neuroncn vaak specifiek op een stimulus in een bepaald deel van het visuele veld (het deel van de wereld dat op het netvlies wordt geprojecteerd). Een neuron zal bijvoorbeeld reageren op een stimulus linksboven in het visuele veld, maar niet op dezelfde stimulus links beneden. Het gebied van het visuele veld waar een neuron op een stimulus reageert heet het klassiek receptief veld. De reactie van een neuron op een stimulus gepresenteerd in dit veld kan echter worden beïnvloed door stimuli die gelijktijdig buiten dit veld gepresenteerd worden. Neuronen met zulk gedrag vertonen een zogenaamde center-surround organisatie. Vaak is de invloed van visuele context op een neuron inhiberend: de respons van een neuron neemt af als stimuli buiten zijn klassiek receptief veld worden gepresenteerd. De mate van inhibitie is afhankelijk van de eigenschappen van stimuli in de

context. Bijvoorbeeld, sterke inhibitie van de respons wordt voornamelijk gevonden als een stimulus dezelfde bewegingsrichting bevat als zijn visuele context. Minder vaak worden neuronen gevonden waarbij de center-surround organisatie faciliterend is. In dat geval neemt de respons van het neuron toe als stimuli buiten het klassiek receptief veld worden gepresenteerd. Dit gedrag van neuronen wordt in dit proefschrift gebruikt als uitgangspunt bij het opstellen van hypothesen over hoe visuele context visuele waarneming beïnvloedt bij de mens.

Bij het bestuderen van de invloed van visuele context op visuele waarneming wordt in de verschillende hoofdstukken gebruik gemaakt binoculaire rivaliteit. Binoculaire rivaliteit treedt op als aan elk van de twee ogen op overlappende plekken een andere stimulus wordt aangeboden (zie Figuur 2 van hoofdstuk 1). In dit geval gebeurt er iets opmerkelijks met de visuele waarneming: het ene moment wordt het ene plaatje (target) waargenomen (dominant), het ander moment het andere plaatje. Dit proces van afwisseling zal voortduren zolang de plaatjes worden aangeboden. Het gebruik van binoculaire rivaliteit biedt de mogelijkheid veranderingen in visuele verwerking van een stimulus op perceptueel niveau te bestuderen. Het veranderen van een eigenschap van een target kan er bijvoorbeeld voor zorgen dat de target langer of minder lang wordt waargenomen. Als regel geldt dat een sterker target langer waargenomen wordt dan een zwakker target; een sterker target is dus meer dominant.

Hoofdstuk 2

In dit hoofdstuk wordt de volgende vraag behandeld: hoe wordt binoculaire rivaliteit tussen twee targets die beweging bevatten beïnvloed door een visuele context die ook beweging bevat? Om deze vraag te beantwoorden werden twee targets gepresenteerd die beweging in tegenovergestelde richting bevatten. Om deze targets heen werd een ring gepresenteerd die beweging bevatte in dezelfde richting als een van de rivaliserende targets. Het toevoegen van de context met beweging zorgde ervoor dat de target met de bewegingsrichting tegenovergesteld aan de context langer werd waargenomen dan de target met beweging in dezelfde richting. De invloed van de bewegingscontext op de rivaliserende targets zou het resultaat kunnen zijn van bovengenoemde center-surround interacties: door center-surround inhibitie neemt de sterkte van de target met dezelfde bewegingsrichting af. Als resultaat hiervan wordt de target met de tegenovergestelde bewegingsrichting als de context langer waargenomen dan de andere target.

Hoofdstuk 3

Is de invloed van visuele context op binoculaire rivaliteit specifiek voor visuele beweging? In hoofdstuk 3 werd de invloed van visuele context op binoculaire rivaliteit bestudeerd voor

beweging, oriëntatie en kleur. Ook onderzochten we of de invloed van visuele context op binoculaire rivaliteit afhankelijk is van contrast. Recente studies hebben aangetoond dat de manier waarop de respons van een neuron beïnvloed wordt door visuele context afhankelijk is van het contrast van de aangeboden stimuli. Is de invloed van een visuele context op binoculaire rivaliteit ook afhankelijk van contrast?

In de experimenten gebruikten we: (1) targets met verschillende oriëntatie omgeven door een ring met dezelfde oriëntatie als een van de twee targets, (2) targets met tegenovergestelde bewegingsrichtingen omgeven door beweging in dezelfde richting als een van de targets en (3) rode en groene targets omgeven door dezelfde kleur als een van de twee targets. In alle condities werd dominantie van de rivaliserende targets beïnvloed door de visuele context. Bij hoog contrast was de target met dezelfde eigenschap als de context (bijvoorbeeld de target met dezelfde oriëntatie) minder dominant dan de target waarvan de eigenschap contrasterend was met de context (bijvoorbeeld de target met de oriëntatie verschillend van die van de context). Dit effect trad op voor alle drie de stimuluseigenschappen. Bij laag contrast was de invloed echter totaal anders: als context en targets waren gedefinieerd door oriëntatie of beweging was bij laag contrast de target met dezelfde eigenschap als de context dominant. Voor stimuli gedefinieerd door kleur was dit niet het geval; bij laag contrast werd dominantie van de targets niet beïnvloed door de context. Deze resultaten komen overeen met recente neurofysiologische bevindingen afkomstig van dierstudies: center-surround interacties treden op bij neuronen die betrokken zijn bij de verwerking van beweging, oriëntatie en kleur. Verder is de manier waarop een context de reactie van neuronen beïnvloedt afhankelijk van contrast: bij hoog contrast overheerst inhibitie, bij laag contrast facilitatie.

Hoofdstuk 4

Wat is de invloed van de grootte van een visuele context op visuele waarneming? In het eerste experiment van hoofdstuk 4 werd de grootte van de context gepresenteerd rond rivaliserende targets gevarieerd. Ook werd het contrast van targets en context gevarieerd. Verandert de invloed van grootte van de context bij verschillende contrasten? De gebruikte rivaliserende targets waren een bewegingstarget en een stationair target. Deze targets werden omgeven door een ring die beweging bevatte in dezelfde of in de tegenovergestelde richting als het bewegingstarget. De resultaten tonen aan dat de grootte van de bewegingscontext een grote invloed heeft op dominantie van de rivaliserende targets: toename in grootte van een context met beweging in dezelfde richting als het bewegingstarget leidde tot een toename in dominantie van de stationaire target. Toename in grootte van de context met beweging in tegenovergestelde richting van de bewegingstarget leidde tot een toename in dominantie van de bewegingstarget. Verder was de invloed van een context met beweging in dezelfde richting als de bewegingstarget groter dan de invloed van een tegenovergestelde bewegingsrichting.

Nadere bestudering van de dominantieduren van de stationaire en de bewegingstarget leverde interessante resultaten op: de invloed die de visuele context had op de dominantieduur van de rivaliserende targets leek sterk op de invloed die het verlagen van het contrast van de bewegingstarget zou hebben op de dominantieduur. Resultaten van dierexperimentele studies suggereren dat center-surround interacties op een vergelijkbare manier de reactie van een neuron op een stimulus beïnvloeden als het verlagen van het contrast van deze stimulus. De invloed van visuele context op binoculaire rivaliteit lijkt dus weer sterk op de invloed van visuele context op de reactie van een neuron.

In het tweede experiment onderzochten we op welke niveaus van visuele verwerking center-surround interacties plaatsvinden. In dierexperimenteel onderzoek zijn center-surround interacties voornamelijk gevonden op het niveau van de mediotemporale cortex (MT). In dit hersengebied is visuele werking voornamelijk binoculair: verwerking is gebaseerd op informatie van de twee ogen. Recent onderzoek laat echter zien dat center-surround interacties ook optreden in de primaire visuele cortex (V1). In dit gebied is visuele verwerking veelal monoculair: informatie van elk oog wordt apart verwerkt.

In dit experiment gebruikten we geen binoculaire rivaliteit. Echter, om verschillende niveaus van visuele verwerking te bestuderen werd een bewegingstarget gepresenteerd aan slechts één van beide ogen. In dit target werd de relatieve sterkte van tegenovergestelde bewegingen gevarieerd. Als de bewegingscomponent naar links sterker was dan de component naar rechts, werd vaker beweging naar links waargenomen. Ook werd een bewegingscontext gepresenteerd aan hetzelfde oog als de target of aan het andere oog. In het eerste geval kan een eventuele invloed van de context op de waargenomen richting van de target veroorzaakt worden door monoculaire en binoculaire verwerkingsniveaus. In het laatste geval kan de invloed alleen een binoculaire invloed hebben: target en context worden immers elk aan een ander oog gepresenteerd.

In beide gevallen leidde het toevoegen van de bewegingscontext ertoe dat de bewegingstarget in de tegenovergestelde richting leek te bewegen. Dit doet de betrokkenheid van center-surround interacties vermoeden: door center-surround inhibitie vermindert het neurale signaal van dezelfde bewegingsrichting. Hierdoor werd vaker de tegenovergestelde bewegingsrichting waargenomen. Echter, een bewegingscontext gepresenteerd aan hetzelfde oog als de bewegingstarget leidde tot een grotere verschuiving van de waargenomen bewegingsrichting van de target dan het toevoegen van de bewegingscontext aan het andere oog. Dit verschil heeft interessante implicaties: Het feit dat de interoculair aangeboden bewegingscontext waarneming van beweging in de target beïnvloedde impliceert de betrokkenheid van binoculaire verwerkingsniveaus. De grotere verschuiving van waargenomen beweging met een monoculair aangeboden context duidt op de betrokkenheid van monoculaire verwerkingsniveaus. Deze resultaten suggereren dat center-surround interacties optreden op meerdere niveaus van visuele bewegingsverwerking.

Hoofdstuk 5

Uit vorige hoofdstukken blijkt dat visuele context perceptuele dominantie van rivaliserende targets kan beïnvloeden. In hoofdstuk 5 wordt de invloed van visuele context op een ander aspect van binoculaire rivaliteit besproken. Volgens een populaire theorie van Blake (1989) is de wisseling van dominantie tijdens binoculaire rivaliteit het resultaat van inhibitoire interacties tussen groepen neuronen in de primaire visuele cortex (V1). In dit gebied wordt input van het linker oog in andere neurale lagen verwerkt als input van het rechter oog. Deze twee groepen neuronen inhiberen elkaar voortdurend. Volgens Blake (1989) is de stimulus gerepresenteerd door de minst geïnhibeerde groep neuronen perceptueel dominant.

Onderzoekers trachten de mate van inhibitie te bepalen door de suppressiediepte te meten. Suppressiediepte wordt bepaald door een taak uit te voeren op de target dat tijdelijk niet dominant is. Door bijvoorbeeld een stimulus met variabele intensiteit op een tijdelijk niet waargenomen target aan te bieden kan bepaald worden hoeveel intensiteit nodig is voordat deze stimulus zichtbaar wordt. Hoe meer intensiteit nodig is om de stimulus zichtbaar te maken, hoe dieper de suppressie.

In een experiment werden een stationair target en een target dat horizontale beweging bevatte gebruikt om binoculaire rivaliteit te veroorzaken. Zodra een proefpersoon aangaf dat de stationaire target perceptueel dominant was (en de bewegende target dus onderdrukt was), werd de beweging van de bewegingstarget kort versneld of vertraagd. De proefpersoon gaf hierna aan of hij of zij versnelling of vertraging waarnam in de bewegingstarget. Door de mate van versnelling of vertraging te variëren kon het punt bepaald worden wanneer de proefpersoon deze taak met een bepaalde prestatie kon uitvoeren. Als de targets werden omgeven door een bewegingscontext was een grotere versnelling of vertraging nodig om tot dezelfde prestatie te komen als zonder bewegingscontext. De suppressiediepte nam dus toe als een bewegingscontext werd toegevoegd. Het toevoegen van een bewegingscontext met dezelfde bewegingsrichting als de bewegingstarget leidde bovendien tot een grotere suppressiediepte dan het toevoegen van een bewegingscontext met tegenovergestelde bewegingsrichting. Deze resultaten tonen aan dat een bewegingscontext suppressiediepte doet toenemen. Het feit dat de context met dezelfde bewegingsrichting leidde tot de grootste toename van suppressiediepte doet vermoeden dat suppressiediepte tijdens binoculaire rivaliteit kan toenemen door center-surround inhibitie.

Hoofdstuk 6

In vorige hoofdstukken werd besproken hoe een visuele context visuele waarneming kan beïnvloeden. Een visuele context kan echter meer of minder relevant zijn voor het uitvoeren van een bepaalde taak. Bijvoorbeeld, het veilig besturen van een auto vereist dat visuele

aandacht over meerdere objecten wordt verdeeld. In dit hoofdstuk staat de volgende vraag centraal: hoe beïnvloedt het uitvoeren van een taak in de visuele context visuele waarneming? Ook om deze vraag te bestuderen gebruikten we binoculaire rivaliteit.

In het eerste experiment werd aan proefpersonen gevraagd twee taken tegelijk uit te voeren. In de eerste taak rapporteerden proefpersonen de dominante waarneming tijdens binoculaire rivaliteit. De tweede taak bestond uit het detecteren van beweging in een ring rond de rivaliserende targets. Deze ring bevatte punten die in willekeurige richting bewogen. Op willekeurige momenten werd in deze ring gedurende korte tijd moeilijk waar te nemen beweging naar links of rechts aangeboden die de proefpersonen moesten detecteren. Uit de resultaten bleek het volgende: De gemiddelde dominantieduur in de rivaliteitstaak was langer wanneer gelijktijdig de bewegingsdetectie taak werd uitgevoerd dan wanneer alleen de rivaliteitstaak werd uitgevoerd. Ook werd de gemiddelde dominantieduur tijdens rivaliteit langer naarmate de bewegingsdetectietaak moeilijker werd.

In het tweede experiment werd de invloed van het uitvoeren van de bewegingsdetectietaak bij verschillende contrasten van de rivaliserende targets onderzocht. Het is bekend dat het verlagen van het contrast van rivaliserende targets de gemiddelde dominantieduur doet toenemen. Naast een toename van gemiddelde dominantieduur met afnemend contrast van de rivaliserende targets zorgde het uitvoeren van de bewegingsdetectietaak tot een extra toename. De invloed van het uitvoeren van de bewegingsdetectietaak op dominantieduur leek sterk op het verlagen van het contrast van de targets; de gemiddelde dominantieduur tijdens uitvoeren van de bewegingsdetectietaak bij een targetcontrast van 50% was gelijk aan de dominantieduur bij een targetcontrast van 100% zonder het uitvoeren van de detectietaak. Dit effect trad ook op bij de andere contrasten. Dit resultaat komt overeen met recente studies waarin wordt beweerd dat aandacht visuele verwerking van een stimulus op een vergelijkbare manier beïnvloedt als het veranderen van het contrast van de stimulus. Dierexperimentele studies hebben bijvoorbeeld aangetoond dat het uitvoeren van een aandachtstaak op een stimulus de neurale respons op deze stimulus op een zelfde manier beïnvloedt als het veranderen van het contrast van de stimulus.

Conclusies

Op basis van de resultaten van de experimenten beschreven in dit proefschrift zijn een aantal conclusies gerechtvaardigd: Visuele context beïnvloedt visuele waarneming tijdens binoculaire rivaliteit. Ook vertoont de manier waarop visuele context binoculaire rivaliteit kan beïnvloeden sterke overeenkomsten met de manier waarop visuele context visuele verwerking op neuronaal niveau beïnvloedt. Verder is de invloed van visuele context op binoculaire rivaliteit afhankelijk van de visuele aandacht betrokken bij het uitvoeren van een taak in de context.

In verschillende experimenten werd aangetoond dat binoculaire rivaliteit wordt beïnvloed door visuele context. Niet alleen kan een visuele context de gemiddelde dominantieduur van rivaliserende targets veranderen, ook kan een context de mate waarin een target wordt onderdrukt beïnvloeden. Dit toont aan dat het proces van wisselende waarneming tijdens binoculaire rivaliteit afhankelijk is van stimuli rond de rivaliserende targets.

De manier waarop visuele context binoculaire rivaliteit kan beïnvloeden lijkt op de manier waarop visuele context de reactie van neuronen moduleert. Dezelfde factoren die de respons van een neuron moduleren, beïnvloeden binoculaire rivaliteit: de overeenkomst in eigenschappen tussen targets en de context, de grootte van de context en het contrast van de targets en de context. Toevoegen van een context met dezelfde eigenschap als een van de rivaliserende targets verlaagde de dominantie van dit target bij hoog contrast. Bij laag contrast verhoogde deze context de dominantie van dit target. Deze bevinding komt overeen met adaptieve center-surround interacties op neuronaal niveau en doet vermoeden dat deze neurale organisatie ook betrokken is bij visuele verwerking bij de mens. Ook suggereren de bevindingen een oplossing voor het volgende probleem: Hoe wordt een visuele stimulus op een efficiënte manier neuraal gecodeerd onder verschillende omstandigheden? Dezelfde stimulus wordt in het ene geval bijvoorbeeld sterk belicht, en in andere geval zwak. Het feit dat de manier waarop context visuele waarneming beïnvloedt afhangt van contrast suggereert een oplossing voor dit probleem. Als het contrast hoog is, wordt het neurale signaal gedempt, als het contrast laag is, wordt het signaal versterkt. Op deze manier kan voorkomen worden dat de reactie op een stimulus te laag is (bij laag contrast), of te hoog (bij hoog contrast). Het lijkt dus dat center-surround interacties een mogelijkheid bieden om een stimulus onder verschillende omstandigheden efficiënt te coderen. Verder suggereert de bevinding dat gelijksoortige resultaten werden gevonden voor stimuli gedefinieerd door beweging, kleur en oriëntatie dat center-surround interacties een algemene eigenschap zijn van visuele verwerking.

Het laatste hoofdstuk toont aan dat de invloed van visuele context op visuele waarneming afhankelijk is van visuele aandacht. Dominantieduren van rivaliserende targets namen toe als proefpersonen een dubbeltaak moesten uitvoeren. Het effect van het uitvoeren van de dubbeltaak had een vergelijkbare invloed op de dominantieduren van de rivaliserende targets als het verlagen van het contrast van de targets. Ook dit resultaat komt overeen met resultaten van dierexperimentele studies: de reactie van een neuron in de visuele cortex op een stimulus kan op een zelfde manier veranderen als gevolg van het uitvoeren van een aandachtstaak als het veranderen van het contrast van de stimulus.

De resultaten van dit proefschrift geven ook inzicht in het fenomeen binoculaire rivaliteit. Het mag duidelijk zijn dat binoculaire rivaliteit sterk beïnvloed kan worden door de visuele context waarin de rivaliserende targets zich bevinden. Ook geven de resultaten inzicht in de rol van aandacht in binoculaire rivaliteit. Uit het laatste hoofdstuk bleek dat dominantieduren tijdens binoculaire rivaliteit afhankelijk zijn van de hoeveelheid aandacht die beschikbaar is

voor het volgen van de rivaliteit: dominantieduren zijn korter als er meer aandacht beschikbaar is voor het volgen van binoculaire rivaliteit. Verder suggereren de resultaten van deze studie dat de mogelijkheid om een dominant percept tijdens binoculaire rivaliteit door aandacht vast te houden begrensd wordt door een laag-niveau effect van visuele aandacht: het aandacht schenken aan rivaliteit verkort de dominantieduren van rivaliserende targets.

Al met al tonen de studies in dit proefschrift aan dat de invloed van visuele context op visuele waarneming sterkt lijkt op de invloed die visuele context heeft op het gedrag van visuele verwerkingsneuronen bij diverse soorten primaten. Hoewel het doorgaans niet mogelijk is het gedrag van individuele neuronnen bij de mens te bestuderen, maken de resultaten van deze studies het waarschijnlijk dat dit gedrag op neuronaal niveau ook verantwoordelijk is voor de invloed van visuele context op visuele waarneming bij de mens.

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Dankwoord

Dank

Promoveren is niet leuk: niks lukt, te dom, is al gedaan. Deze mening deelde ik met enkele kamergenoten: Jan, Mark en Björn. Naast zwelgen in gezamenlijke ellende was het ook nog eens erg gezellig. Zo gezellig dat Jan en Björn vertrokken naar een andere kamer om rustig te kunnen werken. Gelukkig keerde het tij; onderzoeken begonnen te slagen en we kregen meer vertrouwen, niet in de laatste plaats door het niet aflatende enthousiasme van Ryota. Ryota was de afgelopen 4 jaar erg belangrijk voor me, hij gaf belangrijke steun bij het opzetten en uitwerken van verschillende studies. Werken met hem en mijn andere kamergenoten was bijzonder prettig en heeft mooie vriendschappen opgeleverd.

Vertrouwen kreeg ik ook van mijn begeleiders, Frans en Susan. Frans is een enorme motivator. ‘Om jou maak ik me helemaal geen zorgen’, zei hij steeds. Deze steun is erg belangrijk voor me geweest. Verder ben ik dankbaar voor de mogelijkheden die ik kreeg om naar het buitenland te gaan en het enthousiasme voor de wetenschap dat hij op me afstraalde. Ik voel me bevoorrecht bij Frans te promoveren, hij regelt alles perfect voor zijn mensen. Susan wist me altijd goed op schema te houden, met haar maakte ik concrete plannen. Ik ben erg dankbaar voor de structuur die zij aanbracht in mijn werkzaamheden, ik had daar grote behoefte aan. Minstens zo belangrijk tijdens mijn promoveren was Ignace. Alhoewel we het flink oneens konden zijn tijdens wetenschappelijke discussies werd mijn werk er altijd beter van. Ook is hij erg belangrijk geweest voor mijn wetenschappelijke vorming, om het zo maar eens te noemen. Van naïve psycholoog naar volwaardig wetenschapper, mede dankzij hem. Halverwege mijn promotietraject kwam Maarten bij ons werken. Binnen de kortste keren verlost hij me van diverse experimentele problemen. Ook was hij erg belangrijk bij het schrijven van artikelen; hij prikkelde me beter na te denken over veel van mijn beweringen.

Veel leerde ik ook van David Alais, Duje Tadin, Randolph Blake, en Joe Lappin met wie ik samenwerkte. Ook waren zij erg gastvrij toen ik hen bezocht. Het was erg prettig met hen te werken. Verder ben ik Hans Koliijn dankbaar die me hielp bij het bouwen van mijn experimentele opstelling. Als laatste moet ik denken aan Ans, Veronica en Janneke. Ik hoef niemand bij psychonomie te vertellen hoe belangrijk jullie zijn. Dank voor jullie hulp, dropjes en Garfield-stripjes.

Lol

Ik vond het superleuk hier te werken. Tjonge, wat een lol. We stopten Ryota in een papierklike en stuurden hem met de lift naar beneden. Ook gebruikte ik Ryota-in-bureaustoel als bowlingbal en slingerde hem richting een maand voorraad lege flessen aan het eind van de gang. Verder waren we ook heel serieus; we filmde een ronddraaiende taartuitstalling in Hoog Catharijne als ecologisch valide alternatief voor 'structure from motion'. Ook filmde we een roltrap van C&A om een 'implied-motion aftereffect' te kunnen meten. Samen met 'boksbal'-Björn trachtte ik Ignace' dwaze redeneringen te breken, ook al had dit tot gevolg dat half Glasgow erdoor wakker gehouden werd. Als Ignace mijn deo weer eens als vlammenwerper gebruikte verzamelde ik met Ryota wapens (telefoonhoorns, kinsteunen) om deze actie te vergelden. Professioneel waren we ook: tijdens verhitte wetenschappelijke discussies riep iemand van ons steevast wel eens 'Ach, je moet gewoon je bek houden!'.

Vloeken van geluk

Ik ben me erg bewust dat ik het product ben van mijn ouders en hun voorouders. Welke vader staat er met zijn zoon in de tuin door een sterrenkijker te turen en staat 's zondags om 6 uur op om vogels te gaan spotten in het bos in Spaubeek? Dan moet het wel goed komen. Mijn moeder woont in mijn hoofd, en misschien nog ergens anders als de gelovigen toch gelijk hebben. Ik kan niet vaak genoeg vertellen hoe fantastisch ze was, tegen wildvreemden het liefst. Als er lezers zijn die me aardig vinden of zelfs leuk: dat heb ik van haar. Als ik de enige was op deze planeet was er nog altijd mijn zus. Tijdens diepe dalen in de afgelopen 4 jaren was zij er om me daar uit te hengelen. Tja Elge, wat moet ik over jou zeggen? Jij bent mijn favoriete mens en ook nog eens degene met wie ik mijn leven deel. Dit besef doet me vloeken van geluk.

Curriculum Vitae



Christiaan Paffen was born in Spaubeek, the Netherlands on September 9, 1975. After attending primary school in Bingelrade and Hoger Algemeen Voortgezet Onderwijs (HAVO) in Sittard, he moved to Deventer to study Environmental Chemistry at the Hogere Technische School IJselland. After two years he left to study Psychology at the Universiteit Maastricht. During this study he did internships at the Max Planck Institute for Brain Research in Frankfurt am Main, Germany, and at the Regionaal Instituut voor Dyslexie (Regional Institute for Dyslexia). After graduating he left for Utrecht to take a position as a graduate student at the Psychonomics Division of the Helmholtz Institute of the Universiteit Utrecht. During this period he made research visits to the Vanderbilt Vision Research Center of Vanderbilt University in Nashville, Tennessee, USA, as well as the Auditory Neuroscience Department of Sydney University, Australia. From August 2005 on, he will be a post-doctoral researcher at the Psychonomics Department of the Universiteit Utrecht.

