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Eye against eye: How perceived and unperceived visual information interacts

Oog tegen oog: De interacties tussen waargenomen en niet waargenomen visuele informatie

(met een samenvatting in het Nederlands)

Proefschrift

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Eye against eye:

How perceived and unperceived visual information interacts

Sjoerd M. Stuit

All things are subject to interpretation.
Whichever interpretation prevails at a given time is a function of power and not truth
— Friedrich Nietzsche

Table of contents

Chapter 1: General introduction 11

Chapter 2: Orientation-tuned suppression in binocular rivalry reveals general and specific components of rivalry suppression 27

Chapter 3: Suppressed images selectively affect the dominant percept during binocular rivalry 57

Chapter 4: Saliency in a suppressed image affects the spatial origin of perceptual alternations during binocular rivalry 79

Chapter 5: What's grouping during rivalry? 105

Chapter 6: Image-based grouping during binocular rivalry is dictated by eye-of-origin 127

Chapter 7: Summary and Discussion 155

Chapter 8: Nederlandse samenvatting 167

References 181

List of publications 191

Dankwoord / Acknowledgements 193

Curriculum vitae 197

Chapter 1:

General Introduction

A remarkable ability

The visual system has the remarkable ability to turn light, falling on the 2-dimensional surface of the retinas, into a coherent representation of the outside world. This transformation comes so naturally that its complexity often goes unnoticed. However, a massive number of neurons are 'firing' rigorously to convert photons into information about contrast, spatial frequency, orientation, colour, form and motion. And these features are only the basic building blocks of visual perception. They will also be combined at different stages of processing to form more complex representations, such as a purple 1973 Dodge Charger moving at a speed of 150 km/h. The transition from information contained in light to meaningful image representations, occurs in a series of processing stages often referred to as the visual processing hierarchy (Hochstein & Ahissar, 2002). The resulting mental representations form the basis of *what we are aware of*. However, not all processing throughout these stages of the visual hierarchy results in awareness. It remains unclear at what stage processing correlates with our awareness. Addressing this question requires a clear definition of awareness. However, what *constitutes* awareness?

Visual awareness

Research on awareness begins with providing a definition of this capacity of the mind. The terms awareness and consciousness, for instance, are often used interchangeably (e.g. Lamme, 2004; Cohen & Dennett, 2011). In fact, the Merriam-Webster dictionary uses the term 'aware' for their definitions of both consciousness and awareness. Since consciousness is commonly used to describe the state of people who are awake instead of asleep, and we can still *experience* dreams while sleeping, the term consciousness appears less appropriate to refer to the visual experience. To avoid confusion, we will use only the term *awareness* here. Awareness can be defined as the state of perceiving, feeling and/or experiencing sensations (Cohen & Dennett, 2011). As such, awareness is inherently subjective.

Awareness can be further subdivided into phenomenal and access awareness (Block, 2005). Access awareness refers to mental states that can be reported by virtue of high-level cognitive functions such as memory, attention and decision-making. Phenomenal awareness refers to the subjective aspect of experiencing the world, the so-called 'qualia' of visual experience (Block, 2005). In order to study awareness, one requires a tool that allows for different experiences resulting from the same visual information. This ensures that changes in an observer's experience cannot be due to changes in visual input. One such a tool is binocular rivalry, a perceptual phenomenon that can occur under conditions of binocular stimulation.

Binocular fusion and competition

Our eyes view the world from two slightly different viewpoints due to their horizontal offset. The result of these different viewpoints is that the retinal images are not identical. This small difference between the input to left and the right eye is called binocular disparity. These differences are the basis for perceiving stereoscopic depth. However, not all different binocular images can be combined into one single stable percept. When the images presented to the left and the right eye are incompatible, perception starts alternating. That is, the content that one is aware of alternates between the two images presented. This phenomenon is referred to as *binocular rivalry* (Alais & Blake, 2005).

When one is aware of one of the two images engaged in binocular rivalry, this image is referred to as *dominant*. The other image is then referred to as *suppressed*. Under normal viewing conditions, incompatible retinal images will usually involve some sort of occlusion that is only present for one eye. In a laboratory setting, incompatible images can easily be presented to the two eyes by means of a mirror-stereoscope (Figure 1). Observers in such a setting can then be asked to report which image they currently perceive. According to Block's (2005) dichotomy, we are then measuring access awareness. As said, for the study of awareness, binocular rivalry has the advantage of causing multiple different perceptual experiences from a stimulus that does not change. It has been argued that this quality gives binocular rivalry a great potential as a tool to investigate the neural correlates visual awareness (Crick & Koch, 1990). However, a detailed understanding of the processes involved in binocular rivalry is required to fulfil this potential. Unfortunately, the current understanding of these processes is incomplete and contains multiple controversies. In this thesis, we focus on two of these controversies.

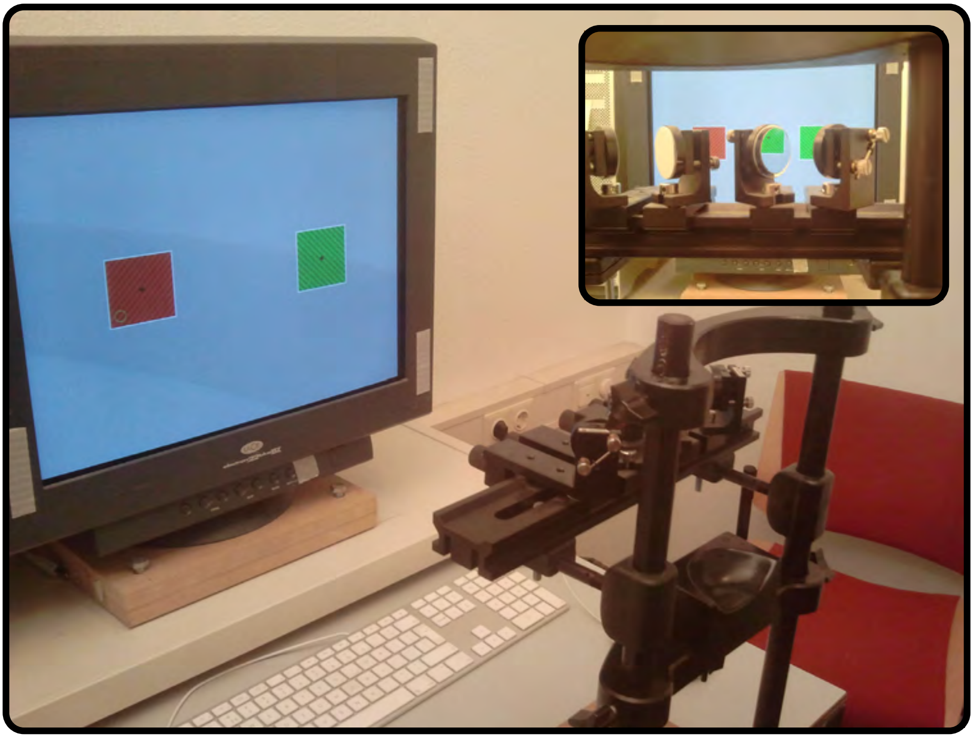

Figure 1:
Photograph of a mirror-stereoscope with an example of a binocular rivalry stimulus. Observers place their head in a chin rest and view the monitor via four small mirrors. The mirrors, seen most clearly in the smaller panel in the upper right corner, change the optical path such that the two images that are next to each other on the screen are presented to corresponding locations on the two retinas.

Current aims

In the current thesis, two unresolved issues that are central to understanding binocular rivalry will be addressed. First, we will focus on the interactions between aware and unaware visual information, a topic that is surrounded by many controversies. For example, there is evidence both in favour of and arguing against binocular suppression as being non-selective. Also, perception during dominance has been argued to be comparable to monocular viewing, yet evidence against this idea is also available. Reconciling these controversial findings is crucial to understand the interactions that result in rivalry suppression and dominance.

Second, we will discuss spatial interactions during rivalry. Although rivalry is a local phenomenon, spatial dependencies do exist. These dependencies reflect influences on binocular rivalry that may originate from different stages along the visual processing hierarchy. The focus is to understand what processing stages are involved, and what their relative contributions are in the instigation of binocular rivalry.

Interactions between perceived and unperceived visual information

Separating the visual input into a part that *will* and a part that *will not* be perceived, is the first step in attaining awareness. As such, rivalry can be viewed as a gating process, only allowing a subset of the information to reach awareness (Figure 2). This leaves the question: is access to unaware information lost completely? More specifically, is all information of the suppressed image suppressed to the same extent?

Quantifying suppression

To investigate whether all information of the suppressed image is removed from awareness to the same extent, one needs to be able to quantify suppression. One way to measure the degree of suppression is to compare sensitivity to a probe presented within the suppressed image and compare that to the sensitivity when that probe is presented within the dominant image. The ratio of these sensitivities is referred to as *the depth of suppression*. For example, a small grating with a specific contrast can be superimposed onto the suppressed image. An observer is then tasked to detect the grating. The same procedure is also followed with the grating superimposed on the dominant image. An observer may need 90% contrast to correctly detect the grating in 75% of the trials when the grating is superimposed on the suppressed image. When

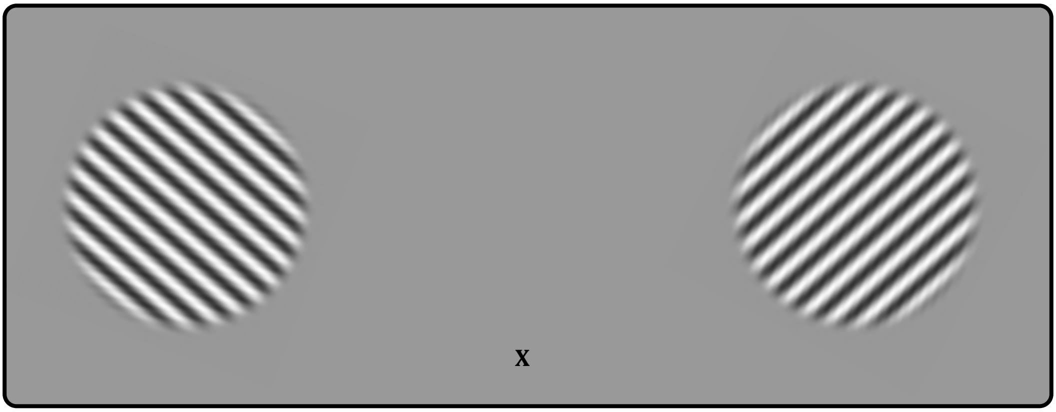

Figure 2:
A quick lesson in 'free fusion' in order to experience binocular rivalry. Hold the figure about 30 cm from your face. Place your index finger on the X and fixate on your fingertip. Now slowly move your finger towards your nose while maintaining fixation, this should result in you looking cross-eyed at your finger. When your finger is roughly 10 cm removed from your nose you should be able to see three gratings instead of two. Without break fixation, shift your attention towards the central grating. Over time, the orientation of the grating will change back and forth. You are now experiencing binocular rivalry.

the grating is superimposed on the dominant image, the observer may only need 35% contrast to detect the grating in 75% of the trials. The ratio of this sensitivity during suppression to dominance is then 0.39 (35/90). The depth of suppression can be used to compare the magnitude of suppression for different image types as well as different image parts.

Uniform suppression during rivalry
How does suppression affect sensitivity to image content? In 1974, Blake & Fox stated that binocular rivalry *non-selectively* suppresses all input to one eye. The idea of non-selectivity in suppression has gained considerable support, resulting in a strong presence in the rivalry literature (e.g. Blake & Fox, 1974; Blake & Lema, 1978; Blake, Westendorf & Overton, 1980; Blake, 1989; Nguyen, Freeman & Wenderoth, 2001; Blake & Logothetis, 2002; Freeman, Nguyen & Alais, 2005). This theory of non-selectivity implies that all features should be affected to the same degree. Although some studies put forward the idea of selective suppression (e.g. Abadi, 1976; O'Shea & Crassini, 1981), these results appeared controversial with an abundance of evidence in favour

of non-selectivity. As such, non-selectivity has remained the dominant interpretation of the nature of perceptual suppression during binocular rivalry (Blake, Westendorf & Overton, 1980; Westendorf, 1989; Blake, 1989; Nguyen, Freeman & Wenderoth, 2001; Blake & Logothetis, 2002) and models of rivalry have dealt with suppression accordingly (Blake, 1989; Wilson, 2003). When taken to the extreme, this notion of non-selective suppression suggests that all visual signals from the suppressed eye (or image) are affected to the same extent for all parts of the competing image. The least extreme version of this notion still implies that when an image is suppressed, all visual signals from the suppressed eye (or image) are removed from awareness. Alternatively, the magnitude of suppression may vary depending on the image content of the competing images.

Relative differences

Since binocular rivalry is based on the presentation of incompatible images to corresponding retinal locations, the relative differences between these images may affect the magnitude of suppression. Intuitively, one might expect suppression to be stronger for two competing images that are very different since identical images tend to fuse. Contrary to this expectation, when the difference in image-content is very large, there may be no suppression at all (Alais & Parker, 2006). Specifically, Alais and Parker (2006) showed that when face stimuli are in rivalry, a probe consisting of a face is suppressed to a much larger degree than a probe containing visual motion. Likewise, a motion probe is more suppressed than a face probe when motion stimuli are in rivalry. These results show that suppression does not affect all information presented to the suppressed eye to the same extent. Instead, suppression appears to be selective, since it does not affect different image types equally. Does this selectivity generalise to variation in suppression for different image parts? Specifically, does selectivity also operate on a finer scale, where suppression is compared for variations within a single feature instead of between different features?

Implications from physiology

From a physiological point of view, a feature-selective form of suppression is very plausible. This is due to the neuronal organization of primary visual cortex. Specifically, this first cortical area receiving visual input contains columns of neurons that respond preferentially to inputs from one eye or the other (Figure 3). Perpendicular to these ‘ocular dominance columns’ are the so-called ‘orientation columns’, containing neurons

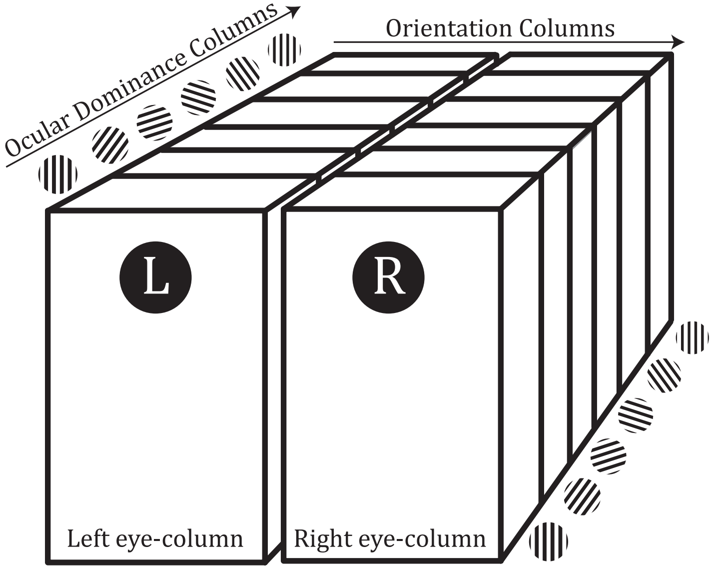

Figure 3: the hypercolumn structure
Neurons in visual area 1 (V1) are proposed to be organized based on their functional properties (Hubel & Wiesel, 1962; Hubel & Wiesel, 1974). The responses of these neurons depend on the orientations and spatial frequencies contained in the visual information in their receptive fields (the location in the visual field to which the neurons can respond). Moreover, some of these neurons also show a preference to the eye to which this information is presented. For instance, one neuron will respond most vigorously to a line presented to the right eye while another responds more vigorously to a line presented to the left eye. This difference in eye-preference is referred to as ocular dominance. Ocular dominance columns are stripes of neurons along the cortical surface that respond preferentially to input from the same eye. Neighbouring columns have an opposing eye-preference. Perpendicular to the ocular dominance columns are orientation columns. These columns have an orientation preference cycle of 180 degrees. Together these two structural properties have been modelled into a hypercolumn structure (Hubel & Wiesel, 1974) where both eyes and all orientations are represented for a particular location in the visual field.

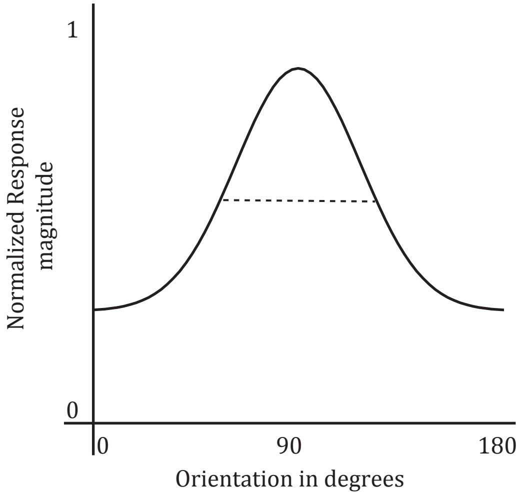

Figure 4:
Schematic representation of orientation tuning in neurons. The solid line represents a neuron's orientation tuning-curve. The peak of the curve is at the neurons preferred orientation, in this case at 90 degrees. The dotted line indicates the bandwidth of the tuning-curve. This bandwidth gives an indication of the selectivity of the neuron. Neurons with narrow bandwidths are referred to as more selective in their responses to oriented lines.

that respond preferentially to a particular orientation (Figure 4). The preferred orientation changes gradually throughout the orientation columns (Hubel & Wiesel, 1974; Kenet et al., 2003). Note that this organization results in neurons with more similar preferences being located closer together in the cortex. This has important implications for the communication between those neurons.

Simultaneous recordings from two neurons have provided insight into the strength of their connections. Importantly, it has been shown that connection strength decreases as a function of cortical distance (Das & Gilbert, 1995; Bosking, Zhang, Schofield & Fitzpatrick, 1997). These findings demonstrate that 1) neurons located closer to each other have stronger connections and, 2) neurons with similar preferences are located closer together than neurons with dissimilar preferences. It follows that neurons that respond to similar feature-content influence each other more than neurons that respond to less similar feature-content. This influence that the neurons have on each other can be either of facilitatory or inhibitory nature. Both facilitatory and inhibitory projections from one neuron to another tend to connect neurons with a similar orientation preference (Dalva, Weliky & Katz, 1997; Buzas, Eysel, Adorjan & Kisvarday, 2001). The combined effect of these connections under dichoptic conditions is particularly relevant to binocular rivalry. Specifically, presenting a preferred together with a non-preferred stimulus dichoptically reduces neural responses relative to the presentation of the preferred stimulus only (Sengpiel & Vorobyov, 2005). In other words, the response to one orientation is reduced by the presence of a second orientation in the same location. Similar to what occurs during binocular rivalry, this is a suppressive interaction between two images in the same location.

Suppressive interactions

So far, evidence has been presented suggesting that suppressive interactions between incompatible images are strongest when they stimulate neurons that share the strongest connections. These connections will be between the neurons located closest together in the cortex and have similar tuning preferences. As a result, suppression during rivalry is expected to be greatest for images that are similar yet still lead to binocular rivalry. If suppression is strongest for more similar images this indicates that it is *not* the non-selective process it is often considered to be (e.g. Blake & Fox, 1974; Blake & Lema, 1978; Blake, Westendorf & Overton, 1980; Blake, 1989; Nguyen, Freeman & Wenderoth, 2001; Blake & Logothetis, 2002; Freeman, Nguyen & Alais, 2005).

A few studies have addressed suppression strength for stimuli of varying orientation. The first study to do so was performed by Abadi (1976), and suggested that rivalry suppression is feature-selective. In this study, gratings were presented dichoptically and observers manipulated the contrast of one of the gratings until it was completely dominant. The results indicate that a grating with similar orientation to that of the grating presented to the other eye requires more contrast to become dominant than one with a very different orientation. O'Shea and Crassini (1981) used a similar approach to test for variation in the magnitude of suppression. They presented orthogonal gratings dichoptically and measured the time it took observers to notice a change in orientation in either the suppressed or the dominant grating. They found an overall increase in reaction times when the test grating was suppressed relative to when it was dominant. Moreover, the reaction times depended on the magnitude of the orientation change.

Based on these results, O'Shea and Crassini (1981) argued that binocular rivalry suppression is sensitive to orientation. A study conducted by Nguyen, Freeman and Wenderoth (2001) also tested for variations in the magnitude of suppression based on varying orientations engaged in rivalry. In contrast to the two aforementioned studies, they found the magnitude of suppression to be constant for all orientation differences. The differences between these studies leave the nature of suppression unclear. In chapter 2, we use a new combination of methods to approach this problem.

Perceptual dominance

A different approach to the problem of selectivity during rivalry suppression is to investigate perception during *dominance*. In line with the non-selective theory, dominance during rivalry has been argued to be comparable to monocular viewing (Blake & Camisa, 1979; Westendorf, 1989; Tsuchiya, Koch, Gilroy & Blake, 2006; Alais & Blake, 2005; Gilroy & Blake, 2004), In other words, perception during rivalry dominance is comparable to perception when there is no stimulus presented to the suppressed eye. However, there are several reports that suggest that information that is suppressed from awareness influences perception of a dominant, or perceived, image. For instance, Treisman (1962) showed that binocular depth perception can coexist with binocular rivalry. This result suggests that at least some of the suppressed signals can survive rivalry suppression to alter perception during dominance. In other words, the suppression of the non-dominant eye was incomplete; some information of the suppressed image was used to allow for the perception of stereoscopic depth.

Carlson and He (2000) used rivalling images with periodic luminance modulations that differed in frequency as well as in orientation. They showed that the frequencies in the two competing images can integrate into binocular beats: a slow flicker amplitude modulation that corresponds to the difference between the two primary frequencies. Again, this finding suggests that not all information from the suppressed image is unavailable for awareness. Pearson and Clifford (2005) provided yet another example of suppressed visual features influencing perception of a dominant image. In their experiment they used rivalling gratings to show that the perceived orientation of a *dominant* grating is systematically biased towards or away from the orientation of a suppressed grating. The direction of the bias depended on the difference in orientation. The magnitude of the difference between the perceived and the physical orientation, as well as the direction of this effect (a clockwise or counterclockwise shift in perceived orientation), depended on the orientation difference between the two competing images. However, the exact relationship between monocular viewing, rivalry dominance and rivalry suppression has yet to be investigated. In Chapter 3, we investigate whether sensitivity to a stimulus during dominance in binocular rivalry is the same as during monocular viewing. In addition, we investigate whether dominant images are affected in a feature-selective manner, similar to what we hypothesized for suppressed images.

Spatial interactions during binocular rivalry

So far we have focused on interactions between aware and unaware information on a local scale. That is, for rivalling information at a fixed location, which is known to the observer. However, when we are *aware of a scene in the world*, we tend to have a global awareness of that scene. Our awareness is generally not limited to a small part of the visual field. In fact, global awareness has been argued to precede awareness of local elements (Hochstein & Ahissar, 2002). Yet during rivalry, an alternation in awareness from one image to another usually starts in one location and gradually spreads across the entire image (Wilson, Blake & Lee, 2001). What determines the location where perceptual dominance begins during rivalry? In chapter 4, we ask if the origins of perceptual alternations are affected by local variations in suppressed images.

Rivalry zones

The gradual spread of transitions from one image to another suggests that the content of rivalry dominance in one location of the visual field is dependent on the content in neighbouring regions. On the other hand, when large images are engaged in rivalry, perception often consists of a patchwork combination of the competing images where different locations have different perceptual outcomes (Meenes, 1930). In other words, the dominant percept contains parts of the left- and right eye's image. This patchwork (also called 'piecemeal') rivalry is absent when the images are rather small (Blake, O'Shea & Mueller, 1992). This difference in patchwork rivalry reveals an important characteristic of rivalry: it is mainly a *local* phenomenon; perceiving a dominant image is the result of the interaction of local zones involved in rivalry. Investigations into this local nature of rivalry revealed that the size of local rivalry zones scales with eccentricity (Blake, et al., 1992). This suggests that the size of rivalry zones corresponds to the size of receptive fields in the hypercolumns of the early visual cortex (Blake, et al., 1992). However, as noted above, alternations tend to start locally and spread gradually to neighbouring regions (Wilson, Blake & Lee, 2001). This suggests that different regions are not completely independent during rivalry. Additional evidence for this claim comes from studies showing that adjacent rivalry zones tend to produce the same dominant percept when neighbouring zones share similar image content such as motion or colour (Whittle, Bloor & Pocock, 1968; Kovács, Papathomas, Yang & Fehér, 1996; Alais & Blake 1998), even when this information is distributed across the two eyes. Such combination of image content distributed across the two eyes is referred to as *grouping during rivalry*.

Grouping during rivalry

Grouping during rivalry based on image content is reminiscent of the theory that competition during rivalry occurs between representations of visual stimuli at a relatively late stage of visual processing (Logothetis, Leopold & Sheinberg, 1996; Kovács, Papathomas, Yang & Fehér, 1996). However, early visual areas already code information about image content (Hubel & Wiesel, 1962; Hubel & Wiesel, 1974). Moreover, two images may also be dominant together because they are presented to the same eye. The relative importance of these cues to grouping is related to the most debated issue concerning binocular rivalry: At what level(s) of processing is rivalry instigated? In short, one side argues that competition is between monocular channels (Figure 3) in primary visual cortex (Eye-based competition; Blake, 1989; Tong & Engel, 2001). The image-based competition theory states that competition during rivalry occurs between representations of images at a relatively late stage of visual processing independent of the eye to which the images are presented (Logothetis, Leopold & Sheinberg, 1996; Kovács, Papathomas, Yang & Fehér, 1996). For example, when the competing images are rapidly relocated between the eyes, observers still report rivalry-like dominance periods that extend the duration of multiple between-eye swaps (Logothetis, Leopold & Sheinberg, 1996; Silver & Logothetis, 2007). The dominance duration of a particular image thus appears unaffected by changing the eye to which it is presented. This finding is, at first sight, at odds with the notion that all inputs to one eye are suppressed from awareness. Moreover, it suggests that competition during rivalry does not necessarily involve monocular channels. However, for binocular rivalry to occur, there needs to be an image difference between the eyes. In other words, both eye-based and image-based competition is always present during binocular rivalry.

Disentangling separate influences

As explained above, the two forms of competition (eye- and image-based) cannot be separated completely. Unable to truly reconcile these theories, and by trying to incorporate many substantially different results, several groups have suggested that rivalry must be resolved at multiple levels of the visual processing hierarchy (Blake & Logothetis, 2002; Silver & Logothetis, 2007; Freeman, 2005; Lee, 2004; Nguyen, Freeman, & Alais, 2003; Wilson, 2003). However, this leaves us with unanswered questions. For instance: What levels are being referred to? Can we quantify the contribution to rivalry at the different levels? What kind of information affects these contributions? In chapter 5, grouping is used as a tool to determine the relative contributions of both eye-based and image-based rivalry to perceptual dominance. In chapter 6, this line of research is continued and we investigated which factors determine the magnitude of these respective eye- and image-based contributions to perceptual dominance.

Summary

When incompatible images are presented to corresponding locations of the retinas, perception alternates between the two images. The image one is aware of is referred to as being dominant, while the other image is then referred to as being suppressed. Suppression has been argued to be a non-selective process, affecting all information equally. However, different aspects of the image may not be affected in the same way. Moreover, residual processing of images, which we are unaware of, may influence perception during rivalry. In this thesis, we will investigate the local interactions between the processing of competing images.

In chapters 2-4 of this thesis, the following questions will be addressed:

- Does the degree of suppression of image features depend on the content of the rivalling images?
- Is sensitivity to image features during dominance the same as during monocular viewing?
- In what way are dominant images affected by suppressed images?
- Is the origin of perceptual alternations affected by local variation in suppressed images?

Next, we will focus on spatial interactions during binocular rivalry. Rivalry has been shown to be a local process but the local dominance is affected by neighbouring regions undergoing rivalry. Moreover, the outcome of rivalry competition has been suggested to depend on multiple stages along the visual processing hierarchy including an early eye-based level and a later pattern- or image-based level. In the chapters 5 & 6 we will address:

- What are the relative contributions of eye- and image-based processing to binocular rivalry?
- Does the contribution of eye- and image-based processing vary as a function of image complexity?

In chapter 7, the findings presented in this thesis will be combined into a general framework of interactions during binocular rivalry.

Chapter 2:

Orientation-tuned suppression in binocular rivalry reveals general and specific components of rivalry suppression

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Abstract

During binocular rivalry (BR), conflicting monocular images are alternately suppressed from awareness. During suppression of an image, contrast sensitivity for probes is reduced by ~.3-.5 log units relative to when the image is in perceptual dominance. Previous studies on rivalry suppression have led to controversies concerning the nature and extent of suppression during BR. We tested for feature-specific suppression using orthogonal rivalling gratings and measuring contrast sensitivity to small grating probes at a range of orientations in a 2-AFC orientation discrimination task. Results indicate that suppression is not uniform across orientations: suppression was much greater for orientations close to that of the suppressed grating. The higher suppression was specific to a narrow range around the suppressed rival grating, with a tuning similar to V1 orientation bandwidths. A similar experiment tested for spatial frequency tuning and found that suppression was stronger for frequencies close to that of the suppressed grating. Interestingly, no tuned suppression was observed when a flicker-and-swap paradigm was used, suggesting that tuned suppression occurs only for lower level, interocular rivalry. Together, the results suggest there are two components to rivalry suppression: a general feature-invariant component, and an additional component specifically tuned to the rivalling features.

Introduction

Presenting conflicting visual information to each eye results in perceptual alternations between the two monocular images such that each undergoes suppression in a stochastic alternation. This phenomenon of fluctuating perception with constant visual input is referred to as binocular rivalry (BR) and has been a popular topic with visual scientists for nearly two hundred years (Wheatstone, 1838). Many different kinds of images will induce BR provided their features differ sufficiently. BR has been demonstrated in many primary stimulus domains, for instance: motion (Moutoussis, Keliris, Kourtzi, & Logothetis, 2005), orientation (Polonsky, Blake, Braun & Heeger, 2000), spatial frequency (Julesz & Miller, 1975), and colour (Breese, 1909), as well as between global motion and complex visual objects such as houses and faces (Tong, Nakayama, Vaughan & Kanwisher, 1998; Alais & Parker, 2006; Alais & Melcher, 2007). Even though the kinds of stimuli used can differ greatly between experiments, the dynamics of BR and the basic phenomenology of perceptual suppression are highly similar. The lack of awareness during suppression and the diversity of stimuli that engage in rivalry have led to two major questions within BR research: where in the brain is rivalry initiated, and what is the fate of the suppressed stimulus?

In an attempt to answer the first question and identify the level at which rivalry occurs, two conflicting theoretical viewpoints on the nature of rivalry suppression have been developed. One theory proposes that BR is a low-level process where there is competition at an early stage between monocular visual channels to determine which eye will dictate perception (Blake, 1989). This view is often referred to as ‘eye-rivalry’ and has been supported by functional imaging studies (Polonsky et al, 2000; Tong & Engel, 2001) as well as psychophysical experiments (Blake & Fox, 1974; Blake, Westendorf & Overton, 1980). The second theory holds that rivalry is a higher-level process that occurs between representations of visual stimuli that compete for conscious expression at a late stage of visual processing. The prime example of this comes from a study employing rapid switches of stimuli between the eyes, where observers reported slow rivalry-like alternations that could not have been due to rivalry between the eyes (Logothetis, Leopold & Sheinberg, 1996; Silver & Logothetis, 2007). This theory of ‘stimulus rivalry’ also has considerable empirical support (Logothetis et al., 1996; Alais, O’Shea, Mesana-Alais & Wilson, 2000) and a general consensus that both theories can coexist is emerging (Blake & Logothetis, 2002; Silver & Logothetis, 2007), with some suggesting that BR suppression may occur at multiple stages along the visual processing pathway (Nguyen, Freeman & Alais, 2003; Wilson, 2003; Lee, 2004; Freeman, 2005).

To investigate the second question – the fate of the suppressed stimulus – a measure is needed that can quantify the extent of rivalry suppression. Suppression strength is usually calculated by measuring a threshold for a brief probe stimulus presented to one eye while it is suppressed, and comparing that with the probe's threshold for the same eye when it is dominant (Fox & Check, 1968). The ratio of dominance to suppression thresholds, when subtracted from unity, gives an index that ranges from zero (no suppression) to 1.0 (complete suppression). Visual sensitivity for detecting probes during suppression is reduced by about ~.3-.5 log units relative to when the image is dominant (Blake & Fox, 1974; O'Shea & Crassini, 1981; Ooi & Loop, 1994), although suppression is generally greater for more complex images (Nguyen et al., 2003; Alais & Parker, 2006; Alais & Melcher, 2007). This typical reduction in sensitivity during suppression corresponds to a suppression strength of ~.41-.52. Suppression strength studies such as these show that signals associated with the suppressed image are not entirely lost even though perception of the suppressed image can be completely absent (Blake, 1989).

Past studies dealing with the nature of rivalry suppression have predominantly argued that it is a nonselective process, with evidence indicating that an eye is insensitive to all stimuli during suppression, not just the suppressed stimulus (Blake et al., 1980). The idea of nonselective suppression has been based on results showing that probes very dissimilar to the rival stimuli were consistently harder to detect in suppression than in dominance (Fox & Check, 1966, 1968; Wales & Fox, 1970). Although this does show that all visual input to the suppressed eye is subject to suppression, it does not necessarily mean that all these inputs are suppressed to the same extent. Previous research has shown that the dominant percept during rivalry can be influenced by the suppressed stimulus in a rather specific manner (Treisman, 1962; Carlson & He, 2000; Andrews & Blakemore, 2002; Pearson & Clifford, 2005). For example, Treisman (1962) showed that different stimulus attributes may combine between the eyes into a percept that is based on a combination of the two competing stimuli. Moreover, Pearson and Clifford (2005) found that, during rivalry of competing orientations, a suppressed orientation systematically biases the perception of the dominant orientation. However, research examining the degree to which suppressed probes are suppressed has led to contradicting results. Several studies have looked at specificity in suppression and while some did show selective suppression effects for high- as well as low-level features (O'Shea & Crassini, 1981; Apthorp, Wenderoth & Alais, 2009; Alais & Parker, 2006), others did not (Nguyen, Freeman & Wenderoth, 2001). For example, although O'Shea and Crassini (1981) found that, during rivalry of differently oriented gratings, small orientation changes in the suppressed image are more suppressed than larger changes, Nguyen and colleagues (2001), also measuring during orientation-based rivalry, found no such effect. An example of high-level feature specificity in rivalry suppression comes from a study by Alais and Parker (2006). They found that, when face-stimuli are in rivalry, a face-probe is much more suppressed than a motion-probe, whereas the motion-probe is more suppressed when motion stimuli are in rivalry. Even though some of these studies show strong evidence for feature specific suppression during BR, suppression is still argued to "operate non-selectively to weaken all inputs to the suppressed eye" (Blake & Logothetis, 2002). With evidence in favour of both selective and non-selective suppression, it's important to examine the nature of suppression more closely. First of all, can we find selectivity in suppression? If so, what is suppression specific to? Moreover, when is suppression specific? If suppression is only selective under certain conditions, this might explain the conflicting results of previous studies examining these questions.

In this study we tested whether suppression during binocular rivalry between orthogonal gratings is uniform across a range of orientations and spatial frequencies, or whether it is specific to the particular features engaged in rivalry. If suppression is uniform, all orientations and spatial frequencies within the rivalry region should be suppressed to a similar extent since it is the eye that is being suppressed. However, if rivalry is specific to the neurons representing the conflicting stimulus inputs, we would expect that probes with features dissimilar to the rivalling stimuli should be easier to detect than probes similar to the rival stimuli. This hypothesis was tested using orthogonal rivalling gratings and by measuring contrast sensitivity to grating probes at a range of orientations and spatial frequencies in a forced-choice probe-orientation task (see Figure 1).

Methods

Observers
A total of 4 observers (3 males and 1 female, mean age: 33), including 3 of the authors, participated in Experiment 1, all having normal or corrected-to-normal vision. All observers were trained in BR and provided informed consent at the start of the study. For all observers, the behaviourally dominant eye was the right.

Apparatus
All stimuli were computed using an Apple G5 computer running system OS X and Matlab software with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). The stimuli were presented on a LaCie Electron Blue 22" (series 3) monitor with a resolution of 1024 x 768 pixels x 75 Hz. All stimuli were presented using a 9-bit colour look-up table that afforded 512 gray levels. This allowed for a more precise measure of probe thresholds at low contrasts compared to the standard 8-bit colour look-up table that affords only half the gray levels. All stimuli were viewed through a mirror stereoscope.

Stimuli
The rival stimuli were two orthogonally oriented sinewave gratings. The gratings were presented at maximum contrast (98% Michelson Contrast, space-average luminance: 37.55 cd/m^2) except for when a probe was presented in it (see below). The rivalling gratings appeared in circular apertures whose edges were softened by a cosine ramp of 0.16° of visual angle on a gray screen (37.55 cd/m^2). The stimuli subtended a diameter of 2° when viewed from the viewing distance of 57 cm. The gratings were oriented ±45° from vertical, with the +45° grating (clockwise from vertical) always presented to the observer's right eyes. Both gratings had a spatial frequency of 3 cpd.

The probe stimuli for Experiment 1 consisted of a small circular sinewave grating (0.65°) that was monocularly presented in the centre of the +45° grating and thus always presented to an observer's right eye. The edge of the probe was spatially smoothed by a cosine ramp (0.32°). The probe was presented in either the dominant or the suppressed image (depending on the condition, see Procedure below) and was smoothly presented over time using a Gaussian cross-fade. Over time, the contrast of the probe first increased and subsequently decreased along a Gaussian profile. The amplitude of the Gaussian corresponded to the probe's contrast and thus varied between trials. The increase in contrast of the probe was mirrored by an equal decrease in the (local) contrast of the rival grating in which it was presented, such that mean luminance and RMS contrast remained constant throughout the transition. This procedure avoided transient increases in contrast, which can disrupt rivalry suppression (Walker, 1978). The Gaussian had a standard deviation of 57 ms and was truncated at ±3.5 standard deviations (±200 ms). The full-width of the Gaussian at half-maximum was 133 ms, and we use this period to define the effective probe duration (the period in which probe contrast was above half-maximum). The probe's orientation ranged from ±10° (close to the probed eye's orientation) to ±45° as follows: ±10°, ±20°, ±30° & ±45°.

Procedure

The two gratings were presented in separate halves of the monitor and viewed through a mirror stereoscope. Observers first aligned the stimuli by adjusting the orientation of the mirrors. Depending on whether the block of trials was a dominance or suppression condition, observers waited for the target stimulus (in which the probe would be presented) to become either completely visible (dominant) or completely invisible (suppressed), after which they triggered the presentation of the probe with a key-press, which was then presented instantly. The orientation of the probe was randomly assigned to be either clockwise or counterclockwise relative to the orientation of the grating in which it was presented. A range of probe orientations was tested in separate blocks to test for orientation tuning. After presentation of the probe the rival stimuli remained present for an additional 300 ms before observers were presented with two adjacent circular gratings showing the two possible responses. Observers indicated which of the two probe orientations had been presented. A schematic diagram of one trial for Experiment 1 is depicted in Figure 1.

In all conditions, the dependent variable was the probe contrast required to perform the probe discrimination task at 75% correct. Contrast was varied using the adaptive Quest procedure (Watson & Pelli, 1983), which effectively varied the amplitude of the Gaussian cross-fade (see Figure 1). Observers first performed in the condition with the probe presented to the dominant eye to become familiar with the task, and performed in at least four Quest staircases for dominance and suppression in an alternating order. The Quest data were then pooled (as were clockwise and counterclockwise probe trials for a given orientation) and fitted with a psychometric function (cumulative

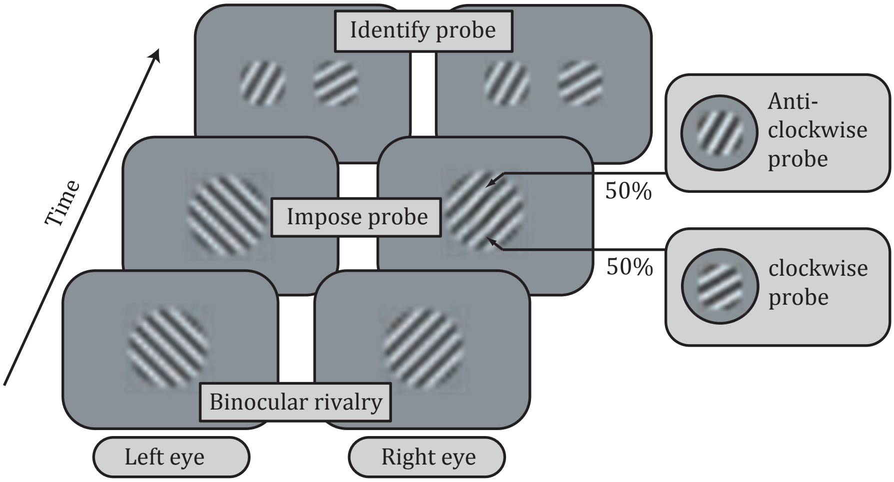

Figure 1: Schematic diagram of the trial sequence in Experiment 1. During binocular rivalry, when the target stimulus is perceived (the right eye's grating in a dominance condition, or the left eye's grating in suppression), the observer initiated probe presentation with a key press. For illustrative purposes, the probe in this example is of much higher contrast than would be used in an actual trial. After presentation of the probe, which was randomly assigned to be either clockwise or counterclockwise relative to the dominant eye's grating, two example gratings are presented and observers signalled with a key press which of the two orientations was presented. Probe presentation was spatially and temporally smoothed to avoid transients (see Methods).

Gaussian) using a maximum likelihood fitting procedure. The strength of suppression was calculated by dividing the 75% correct threshold for dominance by its suppression counterpart and subtracting that value from 1.

Two-factor rivalry suppression model

To test for specificity in orientation suppression we fitted the following Gaussian model to our results:

$$S_{total} = S_{spec} * \exp(-x^2/(2\mu^2)) + S_{gen} \quad (1)$$

The model is simply a Gaussian function with a baseline offset where:

S_{spec} = suppression strength of the specific (tuned) component
S_{gen} = suppression strength of the general (untuned) component
μ = standard deviation of the tuned Gaussian portion
x = the dimension over which the probe varies. In Experiments 1, 3 & 5 the dimension was orientation; in Experiments 2 & 4 the dimension was spatial frequency. At $x = 0$, the probe has the same value as the suppressed grating.

Results

Experiment 1: Orientation discrimination during orientation rivalry.

The aim of Experiment 1 was to determine whether there is an orientation tuning for rivalry suppression by measuring contrast discrimination thresholds for probes presented at a range of orientations. The rival stimuli were orthogonal gratings and the probe stimuli were small centrally presented gratings oriented either clockwise or counterclockwise with respect to the probed eye's grating as described in the Methods section.

Results & Discussion

Data from Experiment 1 are shown in Figure 2, with panel A showing the contrast thresholds for orientation discrimination separately for dominance and suppression conditions. Thresholds for discriminating the probe during suppression show a strong trend to increase as the angular difference between the rival stimulus and the probe grating decreases, with suppression thresholds at 10° being about six times the value of suppression thresholds at 45°. There is also a similar but weaker trend in the dominance thresholds, although this can be attributed mainly to masking at 10°. With such a small orientation difference, the probe's orientation is hard to discriminate when presented in a similarly oriented dominant grating as both would activate the same orientation channel and inevitably lead to an increase in dominance threshold.

More important are the suppression strength indices plotted for each observer in Figure 2 B-E. Suppression strength takes into account variations in dominance threshold by normalizing suppression thresholds relative to dominance thresholds. Effectively, it takes the dominance threshold at each level of orientation difference as a baseline and expresses suppression as a proportionate change from that baseline. Therefore, all suppression strength indices are directly comparable even though probe visibility in dominance changes over orientation. This index clearly shows that suppression is greater for probes oriented close to the orientation of the suppressed grating and reduces in strength as the probe-orientation moves away from the suppressed grating. That is, for probes close to the suppressed grating's orientation, there is a far greater proportionate increase in suppression thresholds. Correspondingly, the data show a significant effect of orientation difference ($F(3,9) = 11.49$, $p < 0.01$), indicating that suppression strength varies depending on the orientation difference between the test probe and the pedestal.

To further investigate the nature of this orientation effect, we fitted our Gaussian model to the data. The R-squares for each observer are indicated in Figure 2 B-E. Our model fits the data well, with r^2 averaging 0.93 across the four observers shown. To remove individual differences in the absolute suppression strengths, we normalized the data to their maximum by dividing each score by the greatest suppression strength index (10°, for each observer). When the normalized data are averaged across observers the fit is improved to $r^2 = 0.99$ (see Figure 2 F for model parameters). These results indicate an orientation tuning function for rivalry suppression that is centred on the suppressed grating's orientation and has a half-width of approximately 26°. For large orientation differences (beyond about 40°), the strength of suppression flattens out to an approximately constant level. Suppression strength, however, does not reach zero even for a 45° orientation difference ($t(3) = 4.86$, $p < 0.01$). Together, these results suggest that while there is significant rivalry suppression at all orientations, there is an additional specific component to rivalry suppression that is tuned to the suppressed grating's orientation.

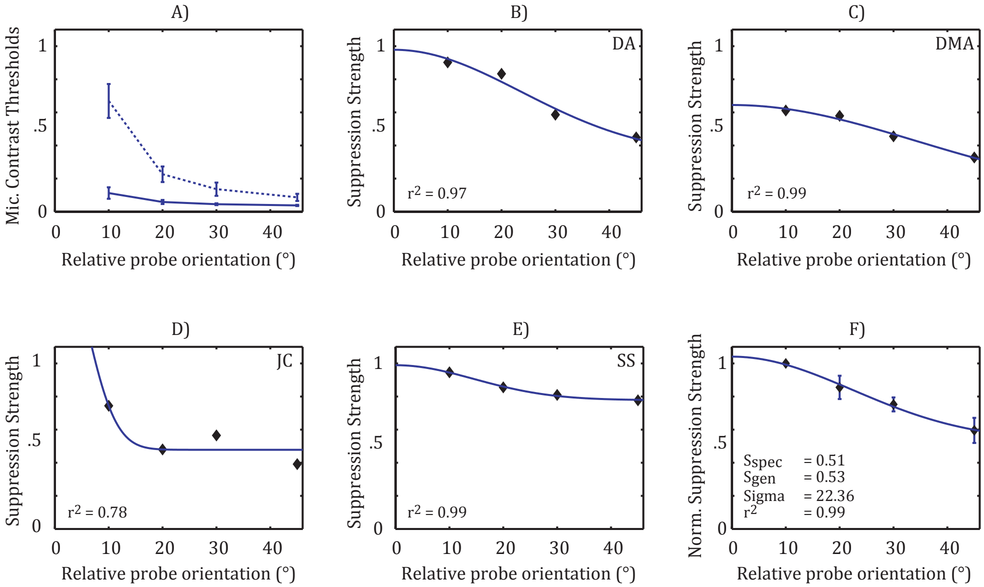

Figure 2: (A) Thresholds for discriminating the probe's orientation during dominance (solid line) and during suppression (dotted line), averaged over observers. Values on the x-axis represent the difference in orientation between the probe and the grating on which it is superimposed. The y-axis represents the contrast threshold (expressed as fraction Michelson contrast) for 75% correct discrimination of the probe. Error bars show ±1 standard error. (B-E) Suppression strength (one minus the ratio of dominance-to-suppression thresholds) is shown for each observer as a function of probe orientation. R-square values indicate fits to our suppression model (see Equation 1, Methods). (F) Suppression strength normalized to the point of greatest suppression (10°, for each observer) and averaged over observers. Error bars show ±1 standard error. Suppression is clearly greatest for the probe orientation closest to the orientation of the suppressed grating and declines with angular difference. Suppression levels off to an approximately constant level beyond about 35°. The continuous line shows the best fit of our suppression strength model, with $r^2 = 0.99$.

Experiment 2: Discriminating probe orientation across spatial frequency

The implication of Experiment 1 is that there is a feature-specific component to rivalry suppression. The goal of Experiment 2 was to extend this result by determining whether suppression during orientation rivalry is tuned to all the features in the rivalling stimuli, or only the conflicting features. Although the rival gratings in Experiment 1 were orthogonally oriented, and therefore conflicted in orientation, they both shared the same spatial frequency (3 cpd) and therefore there was no conflict in the spatial frequency dimension. The question therefore arises: will all features of the suppressed grating undergo a tuned suppression, or only those features that are in interocular conflict? Experiment 2 addresses this question by using the same rival gratings as in Experiment 1 (both 3 cpd) but presenting probes with a range of spatial frequencies (five values spanning 2 octaves). The orientation difference was fixed at ±25°, the phase of the small (0.65°) probe was determined randomly for each trial, and again we measured contrast thresholds for discriminating clockwise from anticlockwise probes. The rest of the methods were the same as for Experiment 1, which are described in detail in the methods section. If the evidence for tuned suppression found in Experiment 1 is limited to the conflicting stimulus dimension, then we would expect to find no tuning for probe spatial frequency. If, however, there is tuned suppression for all features of the suppressed stimulus, then probes should become more suppressed as spatial frequency approaches that of the rivalling gratings.

Results and Discussion

Figure 3 plots the results from Experiment 2, with the contrast thresholds for dominance and suppression on the orientation discrimination task shown in 3A, and the suppression strength indices shown in 3B-F. Looking at the mean dominance thresholds (Figure 3 A), it is clear that there is little variation in probe visibility across spatial frequency. There is a tendency for thresholds at lower spatial frequencies to be slightly higher, although this effect is probably due to fewer cycles of the probe grating being visible within the aperture, which tends to make orientation judgments more difficult. For the most part, however, this trend is echoed by equivalent proportionate changes in the suppression thresholds over probe spatial frequency, so that the suppression indices do not vary much over spatial frequency. The mean normalized suppression strength data (Figure 3 F) does show a significant spatial frequency effect ($F(4,12) = 3.56$, $p < 0.05$), although this does not appear to be due to tuning. Neither the individual data (Figure 3 B-E) nor the average data fitted our Gaussian model well (r^2 (average data) = 0.02). The data fitted better to a standard linear regression model (r^2= 0.69) although the fit was still only modest. Note that the plus and minus 1 octave range of spatial frequencies differences tested should be more than sufficient to reveal evidence of spatial tuning as estimates of the width of spatial frequency channels in humans and primate indicate that they have a full bandwidth of between 1 and 1.5 octaves (Blakemore & Campbell, 1969; De Valois, Albrecht & Thorell, 1982; Wilson & Gelb, 1984). Notably, even the probe showing the least suppression (1 cpd) still had a suppression strength index that was significantly greater than zero ($t(3) = 4.71$, $p < 0.01$), confirming the existence of a general component in rivalry suppression.

Overall, in the absence of a tuning function centred on the frequency of the rival gratings, we conclude that there is no evidence of rivalry suppression being specifically tuned to the spatial frequency of the rival gratings. We therefore suggest that tuned suppression during binocular rivalry may be limited to features that are driving the interocular conflict. However, an alternative interpretation for the lack of tuning is that the orientation difference between probe and target (±25°) was too large for any tuning in spatial frequency to occur: tuned suppression is at an intermediate level for this orientation difference in Experiment 1. It therefore remains possible that the amount of spatial frequency tuning is dependent on the orientation difference between the rival gratings. Still, at least for the settings used here, spatial frequency tuning is absent when an orientation difference is driving the interocular conflict. In Experiment 4, we return to the issue of feature-selectivity in suppression.

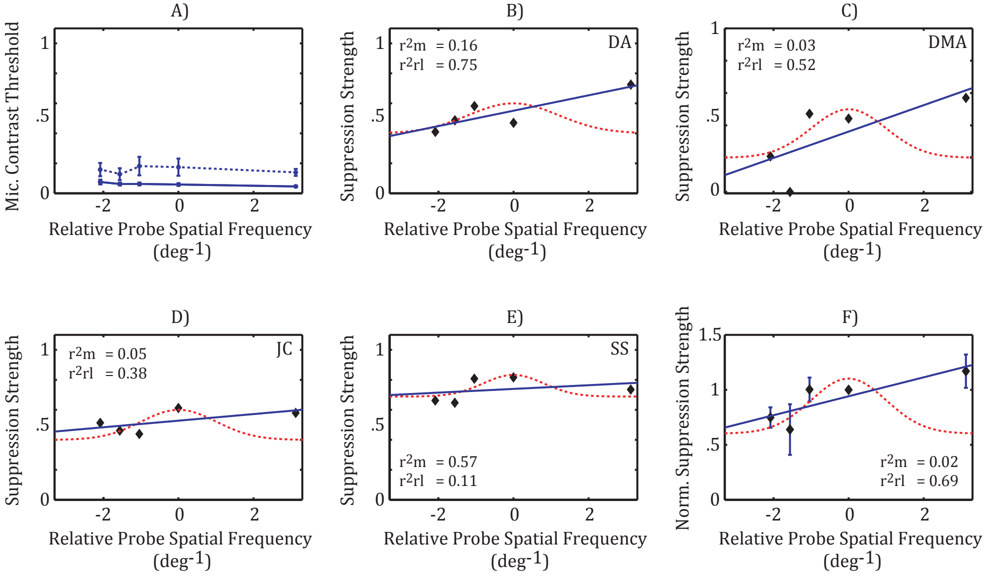

Figure 3: (A) Thresholds, averaged across observers, for discriminating the probe's orientation during dominance (solid line) and during suppression (dotted line) as a function of probe spatial frequency. The rival gratings both had a spatial frequency of 3 cpd. (B-E) Strength of probe suppression across a range of probe spatial frequencies for each observer. The dotted lines indicate the tuned suppression model's fit to each subject's data. Solid lines represent each observer's data's fit to a standard regression line. R-square-values of both the suppression model (r^2m) and regression line (r^2rl) are shown in the for each observer. Note that our tuning model does not fit the data. Linear regression provides better fits for most observers although the r-square values are still only modest. (F) Average suppression strength across observers' normalized data. The data were normalized to the 3 cpd probe score. Error bars represent the standard error of the mean. Again note that our suppression-model does not fit the data well (r^2: .02, S_{spec}: .5, S_{gen}: .6, μ: 1). The regression line, however, does show a modest fit (r^2: .69, slope: .09, offset: .94). The data show significant suppression at all spatial frequencies but no clear tuning function over a 2-octave range of spatial frequency.

Experiment 3: Controlling for centre-surround effects.

Experiment 3 tests an alternative interpretation of the results presented so far, specifically, that the results might be explicable in terms of centre-surround inhibition. In Experiment 2, where the probe was fixed in orientation at ±25°, there was no tuning, yet there was a clear tuning observed in Experiment 1 where the probe varied in orientation. Indeed, the tuning in Experiment 1 peaked when the central probe was nearly collinear with the surrounding rival grating. This suggests an alternative interpretation of the data based on centre-surround interactions. It is well established neurophysiologically that orientation-selective neurons driven by their preferred stimulus become suppressed when an iso-oriented surround is added (Jones et al., 2001). This is similar to the stimulus configuration that produced the strongest suppression in Experiment 1, and suppression due to centre-surround interactions such as these have been shown to combine with rivalry suppression to alter visibility of targets during rivalry (Paffen et al., 2005; Paffen et al., 2006). Potentially, the 'tuning' of rivalry suppression found in Experiment 1 could be due to rivalry suppression combining with a strengthening iso-orientation inhibition as the probe stimulus moves closer in orientation to the surround stimulus. In Experiment 3, we test this possibility by using a larger probe (2°) that is the same size as the rival stimuli. This allows us to present the probe without it being embedded in a surround grating and therefore removes any effect of separate centre and surround regions with different orientations. Probe-orientations used were ±10°, ±25° & ±45°. Stimuli were presented using a 9-bit colour look-up table. Remaining methods are as described in the methods section.

Results and discussion

The data from Experiment 3 using the large full-field probes are plotted in Figure 4. Similar to our first experiment we find a main effect for orientation difference ($F(2,6) = 14.19$, $p < 0.01$) and significant suppression for even the least suppressed orientation difference of 45° ($t(3) = 19.53$, $p < 0.01$). The suppression strength data (Figure 4 F) replicates the orientation-tuned rivalry suppression observed in Experiment 1 and the data showed a good fit to the same model as used for Experiment 1 ($r^2 = 1$). These results confirm that the orientation tuning seen in Experiment 1 is not due to the addition of iso-orientation surround suppression when the central probe and surround grating are nearly collinear.

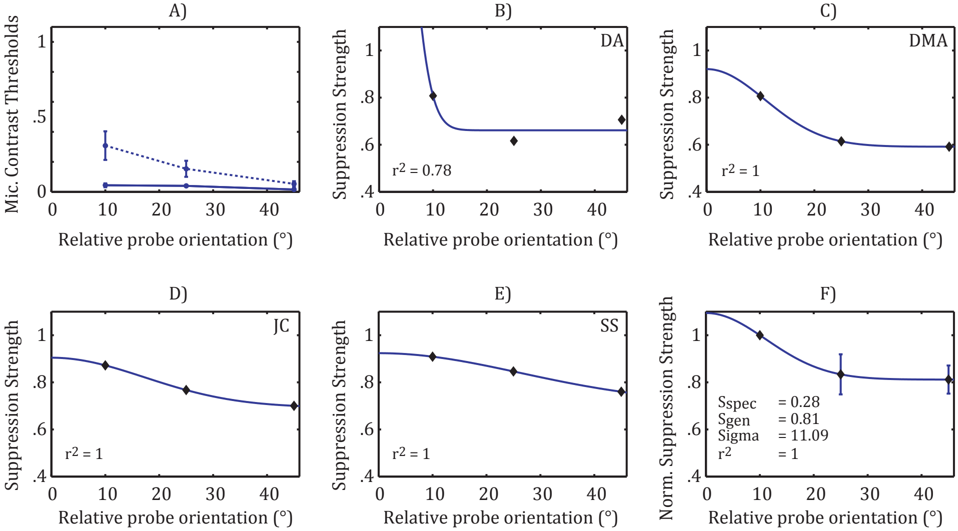

Figure 4: (A) Data from Experiment 3 showing average probe discrimination thresholds for the large (full-field) probe as a function of probe orientation. Dominance thresholds are represented by the solid line and suppression data by the dotted line. The y-axis represents the contrast threshold (expressed as fraction Michelson contrast) for 75% correct discrimination of the probe. The x-axis shows the orientation difference between the probe and suppressed grating. Error bars represent standard errors. (B-E) Suppression strength data per subject. R-square values indicate model fit values. (F) Averaged normalized suppression strength data. Error bars represent the standard deviation of the mean and model fit is depicted in the lower left corner. Suppression deepens for orientations close to that of the suppressed grating, replicating the orientation tuning result from Experiment 1.

Experiment 4: Probe discrimination during 'spatial frequency' rivalry

Having shown that the orientation tuning found for rivalry suppression in Experiment 1 cannot be due to any centre-surround effect interacting with rivalry suppression, we now focus on the lack of spatial frequency tuning for Experiment 2. This lack of tuning can be explained by several possible accounts. One is that there is simply no selectivity in the inhibition between monocular spatial frequency channels. Also, the lack of tuning in Experiment 2 could have been due to a floor effect in suppression. Since we used a probe-orientation that showed relatively little specific suppression in Experiment 1, suppression may have been to weak to show any signs of specificity. Another possibility, however, is that rivalry suppression is only specifically tuned to spatial frequency when spatial frequency is the main source of the interocular conflict. The failure to find spatial tuning in Experiment 2 might simply be a consequence of the fact that the two rival stimuli shared the same spatial frequency. Experiment 4 was designed to dissociate between these possible interpretations. The experiment measured probe orientation discrimination at a range of probe spatial frequencies during rivalry between gratings that differ in spatial frequency. The aim was to test whether rivalry suppression exhibits a specific spatial frequency tuning around the spatial frequency of the suppressed image. This experiment used a pair of gratings that were both oriented +45° from vertical in order to remove interocular orientation conflict. Rivalry between these gratings was induced by adding an interocular spatial frequency difference. In one version, we used 0.75 and 1.5 cpd for the rival gratings, with the probe presented to the eye receiving the high spatial frequency grating. This was referred to as Experiment 4A, and all probes were higher than the 1.5 cpd of the probed eye to provide an upper half-tuning for spatial frequency. In a second version we used rival gratings of 1.5 and 3 cpd with the probe presented to the low spatial frequency grating. This was referred to as Experiment 4B, and all probes were lower than the 1.5 cpd of the probed eye to provide the lower half-tuning around the suppressed grating. Probe size was increased to 1.4° to make sure that the lowest spatial frequency probes contained enough orientation information to do the task, which was to judge whether the probe (randomly either ±25° from the probed grating's orientation) was clockwise or counterclockwise with respect to the suppressed grating. Both versions were presented using a 10-bit colour lookup table. All other aspects of this experiment were similar to Experiment 2.

Results and Discussion

In Figure 5, results from our two half-tuning experiments (Experiments 4A&B) are combined and expressed as suppression strength indices plotted across the seven probe spatial frequencies. Although there were 4 observers, observer JC could not do the task at the very low spatial frequencies (Experiment 4B) due to a recurring lack of rivalry. For this reason, those data points were not included in the group mean analysis and only the four points visible in Figure 5 D were included in the group means. Despite this, the pattern of data is clear and shows strong evidence of spatial tuning (Figure 5 F). The effect of probe spatial frequency was significant in both versions of Experiment 4: $F(3,9) = 4.24$, $p < 0.05$) for Experiment 4A; $F(3,6) = 22.05$, $p < 0.05$ for Experiment 4B. As in the previous experiments, suppression strength was always significantly greater than zero even beyond the tuned portion (see Figure 5 F).

These results show that when a low and a high spatial frequency are engaged in rivalry, adding a probe to the low frequency grating shows a clear suppression tuning for probes of lower spatial frequency. Conversely, adding a probe to the high frequency grating and testing for suppression at even higher spatial frequencies shows a corresponding tuning to higher spatial frequencies. In each case, suppression strength decreases as the probe frequency moves away from the frequency of the probed grating. Together with the results from Experiment 2, the implication is that there are specific inhibitory connections between monocular spatial frequency channels, and that binocular rivalry will not specifically suppress a particular spatial frequency channel unless there is spatial frequency conflict between the rival images. In such a case, it appears that rivalry suppression involves targeted suppression of a particular spatial frequency, which acts in combination with an untuned general suppression. In contrast, if there is no spatial frequency conflict (as in Experiment 2), there is only a general component to rivalry suppression that is weaker but applies to all spatial frequencies approximately equally. When spatial frequency conflict exists, a tuned suppression component centred near the suppressed spatial frequency is added to the general suppression.

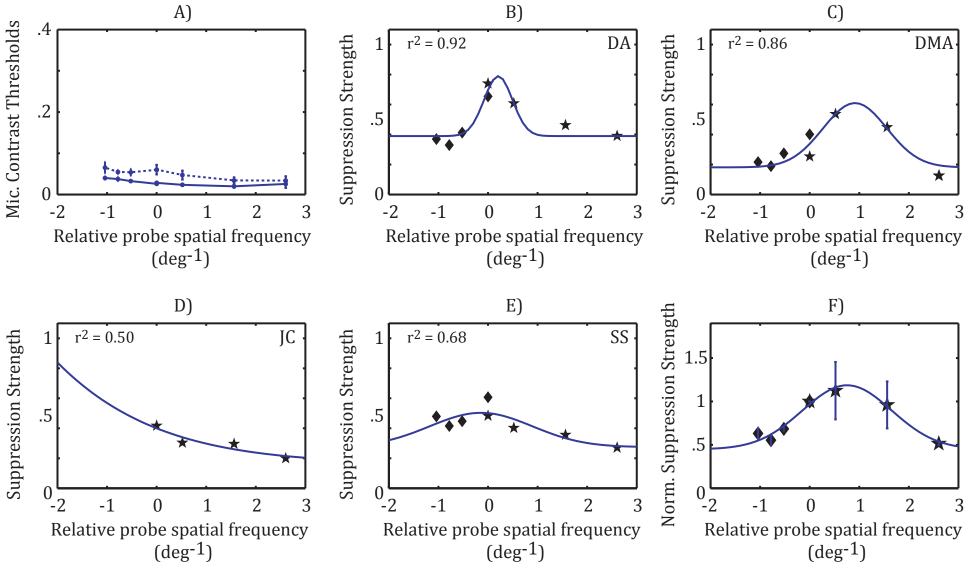

Figure 5: (A) Combined data from Experiment 4-A and -B showing average probe discrimination thresholds as a function of spatial frequency. The solid line indicates the dominance thresholds and the dotted line the suppression thresholds. (B-E) Suppression strength data from both versions of Experiment 4 combined per observer. Stars refer to data from Experiment 4A and Diamonds to 4B. R-square values, indicating model fit are presented in the graphs. (F) Averaged normalized suppression strength data across observers. Error bars indicate standard errors. The data have been fitted with the same model as Equation 1 with the modification of leaving x as a free parameter (r^2: .96, S_{spec}: .74, S_{gen}: .45, μ: 90). Panel F shows a decrease in suppression strength for probes decreasing in spatial frequency when they are presented within a low spatial frequency grating (compared to a grating with a higher spatial frequency; black diamonds). When the probes are imposed on a high spatial frequency grating (relative to its rivalling counter-part; black stars), increasing the spatial frequency of the probes will also lead to a decrease in suppression strength indicating that, when spatial frequency is in conflict, suppression is tuned around a spatial frequency approximating that of the suppressed grating.

Experiment 5: No orientation-tuned suppression for 'flicker-and-swap' rivalry

Rapid interocular switching of rival stimuli has been used to demonstrate that a form of binocular rivalry can occur that must entail processes beyond the early interactions between monocular channels thought to underlie conventional binocular rivalry (Blake, 1989). Often known as flicker-and-swap rivalry, this demonstrates that perceptual alternations can arise independently of the eye-of-origin (Logothetis et al., 1996). In Experiment 5 we test whether flicker-and-swap rivalry produces a similar orientation tuning for rivalry suppression to that observed in Experiment 1 for conventional rivalry stimuli. Since flicker-and-swap rivalry must involve binocular levels of processing that operate without regard to eye-of-origin (Logothetis et al., 1996) and is not tied to early interocular interactions as in conventional rivalry (Tong & Engel, 2001; Pearson, Tadin & Blake, 2007), we expect that tuning to the suppressed orientation will be weaker than observed for conventional rivalry. The reasoning behind this prediction is that orientation tuning-functions become progressively broader after V1 (Desimone, Albrecht, Gross & Bruce, 1984; Desimone, Schein, Moran, & Ungerleider, 1985), resulting in progressively weaker tuning in suppression when rivalry is instigated at relatively late levels of visual processing.

Experiment 5 used interocular 'flicker-and-swap' rivalry (Logothetis et al., 1996). To optimize the strength of perceptual alternations the stimulus parameters chosen closely matched those used by Logothetis et al. (1996), confirmed by Lee and Blake (1999) to be optimal for producing flicker-and-swap rivalry. The stimuli were orthogonally oriented gratings with the same orientation and spatial frequency as described in the general methods section, however, the size of the apertures was increased slightly (2.4° in diameter). The probe-orientations used in this experiment were the same as in Experiment 1 with the addition of probes oriented ±60, ±70 and ±80° away from the suppressed grating. Probe diameter and spatial frequency remained similar to Experiment 1 (0.65°, 3 cpd). The effective probe duration, defined as the full-width at half-maximum of the temporal Gaussian used to presented the probe, was 125 ms. However, because the stimuli underwent on-off flicker, probe duration times were doubled leading to a total presentation time of 250 ms (of which the total "on" time was 125 ms). The gratings were coloured (one red (x = 470, y = 287, 8.97 cd/m^2) the other green (x = 273, y = 506, 27.06 cd/m^2)), as in Logothetis et al., 1996) and flickered continuously at a rate of 18.75 Hz while also swapped between their screen positions (and thus between eyes) every 210 ms. Both gratings were presented at 28% contrast using a standard 8-bit colour lookup table. Unlike the other experiments, the probe could not be exclusively combined with the observer's dominant eye. Instead, the colour-matched probe followed the stimulus with which it was being combined (always the +45° grating) and thus swapped eye every 210 ms in synchrony with the probed grating. Also, because a probe would not be presented in isolation, the presentation of the probe was delayed if an observer made a response during the 'off-phase' of the flickering gratings. The delay had a maximum duration of 53 ms. Because of this potential delay and increased duration of probe presentation, observers were given the opportunity, via key press, to abort trials if perception alternated before, or during, the presentation of the probe. Observer DMA did not take part is this Experiment on account of not displaying any stimulus rivalry.

Results and discussion

The data from Experiment 5, plotted in Figure 6, do not show a main effect for orientation difference, in contrast to what was found in Experiment 1 ($F(6,12) = 1.68$, $p = 0.209$). This shows there is no significant difference between suppression strengths exerted on test probes at any of the tested orientations, indicating that suppression in the case of flicker-and-swap rivalry is not tuned to the orientation of the suppressed stimulus. This can be seen in the values of suppression strength being roughly constant across all probe orientations within 45° of the suppressed orientation. If suppression in flicker-and-swap rivalry were orientation tuned, there would be clear evidence of increasing suppression strength as the probe orientation difference decreased, particular at values of 10° and 20°, yet this did not occur. Similarly, for probe orientations more than 45° from the suppressed orientation, suppression strength shows no orientation tuning.

Overall, there are two key differences that emerge between suppression in conventional rivalry and in flicker-and-swap rivalry. The first is that suppression is not feature-tuned (at least for orientation) in the case of flicker-and-swap rivalry, and the second is that suppression is relatively weak in flicker-and-swap. The point regarding weak suppression in flicker-and-swap rivalry (evident when comparing suppression strength for the two types of rivalry in Figures 2 & 6) confirms the same finding in a recent report on suppression in flicker-and-swap rivalry (Bhardwaj, O'Shea, Alais & Parker, 2008). The lack of specificity for rivalry suppression in the flicker-and-swap paradigm suggests that it does not occur at the stage of early cortical processing where neurons exhibit tight tunings for orientation. In V4, for example, orientation tunings are broader

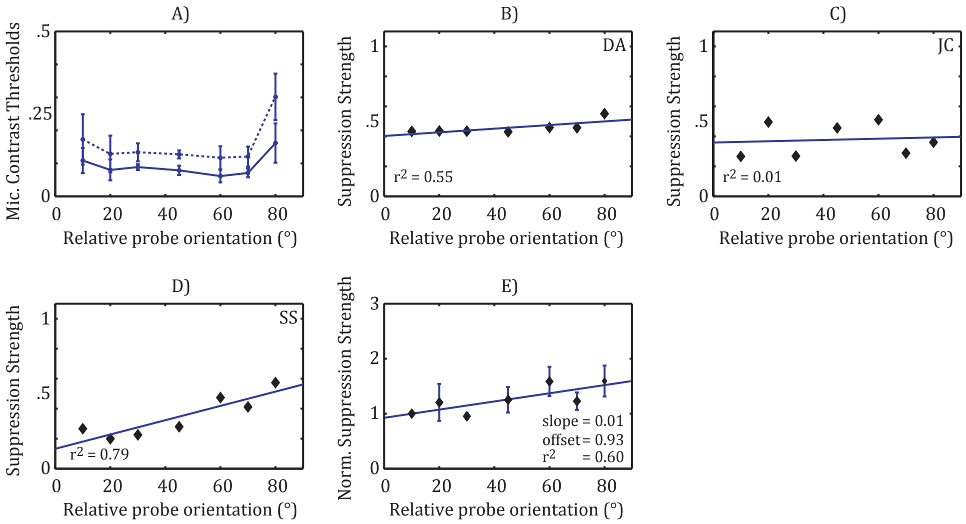

Figure 6: (A) Averaged probe discrimination thresholds as a function of orientation during 'flicker-and-swap' rivalry. The solid line indicates dominance thresholds and the dotted line represents the suppression thresholds. (B-D) Data from Experiment 4 showing suppression strength in flicker-and-swap rivalry as a function of probe orientation for each observer. R-square values, representing the fit to a standard linear regression model are presented in the lower left corners. Note that, compared to results from Experiment 1 and 3, suppression appears to be much weaker for flicker-and-swap rivalry than for conventional rivalry. (E) Normalized suppression data averaged across observers. Error bars represent the standard error and fit parameters to a standard regression model are presented in the lower right corner of the graph. Comparing across the data sets (Experiment 1 and 3) for probes, it is clear that there is no orientation tuning for flicker-and-swap rivalry.

(Desimone, Schein, Moran, & Ungerleider, 1985) and in IT such tuning is present in only a minority of neurons (Desimone, Albrecht, Gross & Bruce, 1984). This, together with the fact that it must involve a binocular substrate suggests that flicker-and-swap rivalry occurs at a later stage of processing than conventional binocular rivalry. This ties in with other recent evidence for a late site for flicker-and-swap rivalry showing that TMS pulses over occipital cortex tend to induce dominance switches for conventional rivalry but not for flicker-and-swap rivalry (Pearson, Tadin & Blake, 2007).

General Discussion

In this paper we have tested whether binocular rivalry suppression is specific to the stimulus features engaged in rivalry or whether it entails a nonselective suppression operating over the rivalry region in a non-selective manner. Our results clearly support the claim that rivalry suppression is selective because plots of suppression strength for orientation and spatial frequency rivalry (Figures 2 & 5) exhibit clear tunings that peak at the value of the suppressed features. Probes similar to the feature driving the interocular conflict (e.g. orientation or spatial frequency), required much more contrast to become visible than did gratings that were further away along these feature dimensions. Importantly, however, there is no value of orientation or spatial frequency in the tunings in Figures 2 and 5 that failed to produce significant rivalry suppression. Therefore, our results do not entirely rule out the alternative position of non-selective suppression. That is, although the strong evidence of tuned suppression rules out the wholesale suppression proposal in its strongest form, there clearly is a component of untuned rivalry suppression. This is evident by the fact that rivalry suppression remains significant at all points beyond the tuned portion of the suppression strength plots. The clear implication of these results is that rivalry suppression involves two components. According to this two-component theory of rivalry suppression, there is a general component that acts non-selectively to uniformly suppress the rivalrous region of the suppressed image, and a specific component that is selectively tuned to the features driving the interocular conflict within that rivalrous region. We suggest that the increasing strength of suppression within the tuned portion of the suppression strength curves is due to the specific suppression component combining with the general suppression component.

An alternative explanation of our results that does not involve the tuning of suppression is that any tuning effect found is due to an apparent motion signal associated with the probes used in the experiments. Even though the probes had a smooth temporal onset, one might perceive apparent motion signals. As the orientation or spatial frequency changes increase, the apparent motion becomes greater and thresholds might decrease, producing a tuning curve in the results. The lack of tuning found in Experiment 5 may be based on the lack of, or degraded, apparent motion effects due to the transient nature of the Flicker-and-Swap stimulus. However, apparent motion does not appear to be a causal factor in the results presented in this paper. Any apparent motion effects should affect performance during dominance as well as suppression. Using suppression depth as our index should control for the apparent motion effects, since it expresses performance during suppression relative to that during dominance. However, apparent motion itself may be affected by suppression in such away that would lead to a tuning function in our experiments. Results from experiments 2 and 4 suggest this is not the case. Since any apparent motion would have been the same for each condition of Experiment 2, the lack of tuning does indeed correspond to an explanation of our tuning results by apparent motion. Yet, in Experiment 4, using the exact same probe, we did find tuning. This argues against the idea that apparent motion is responsible for tuning in suppression.

It has previously been asserted in several influential rivalry reviews that rivalry suppression acts non-selectively (Blake, 1989; Blake, 2001; Blake & Logothetis, 2002). By this it is meant that suppression is not limited to the features of the suppressed image, which obviously disappear from awareness, but may also include many other kinds of stimuli unrelated to the rivalling images. The evidence in support of this has a long history and goes back to Fox's original probe studies (Fox & Check, 1968; Wales & Fox, 1970; Fox & Check, 1972; Blake & Fox, 1974) where it was shown that a probe stimulus superimposed on a rival target was harder to detect in suppression than in dominance, even when the probe was quite unrelated to the suppressed image. In some of these studies (Fox & Check, 1968; Blake & Fox, 1974), the dependent measure was the reaction time to detect the probe (and was found to increase in suppression), whereas in others it was detection thresholds for probes such as spots of light (Blake & Camisa, 1977; Smith, Levi, Harwerth & White, 1982). These studies concluded that rivalry suppression is not limited to the features of the suppressed image. Although Blake and Fox (1974) did find a spatial frequency effect on suppression, no evidence for feature-specific tuning of suppression to the conflicting spatial frequencies was found.

The experiments we report in this paper were designed to systematically test the tuned suppression hypothesis with respect to orientation and spatial frequency. Our results provide clear support for feature-specific suppression, and our study stands out as a rare attempt to explicitly test this hypothesis. Two other studies have attempted a similar investigation of rivalry suppression. The first was conducted by O'Shea and Crassini (1981) and used a rather different approach from ours. Their study included two tasks. In the first, orthogonal gratings were presented dichoptically and observers responded as soon as possible to a change in orientation in either the suppressed or the dominant grating. An 80° range of test orientations was used. An overall increase in reaction times was found when the test grating was suppressed relative to when it was dominant with a greater increase found for larger orientation changes. The second experiment O'Shea and Crassini presented used a 2AFC paradigm where observers had to detect a change in orientation. Surprisingly, performance for orientation changes between 20° and 70° were identical for both suppression and dominance. However, for orientation changes outside this range, performance during suppression declined relative to dominance. O'Shea and Crassini argued that binocular rivalry suppression is sensitive to orientation, reaching a similar conclusion to ours. Important differences with our study are that: (i) we used a depth of suppression paradigm, which gives the suppression performance relative to dominance performance, and (ii) the extension of our results to a tuned suppression effect for spatial frequency.

The second study that attempted a similar investigation was conducted by Nguyen, Freeman and Wenderoth (2001), who included among a series of rivalry studies an experiment designed to test for orientation tuning of rivalry suppression, and another testing for spatial frequency tuning. Their spatial frequency study was similar to our Experiment 2 in which the two rival gratings had the same spatial frequency and, as in our experiment, no tuning was found for spatial frequency. They did not, however, include an experiment like our Experiment 4, in which there was spatial frequency conflict between the rival gratings and which did produce tuned suppression. Their study of orientation tuning for suppression was similar to our Experiment 1 but their results were equivocal. Of the three observers tested, one appeared to show some orientation tuning. Overall, however, the group effect was not statistically significant and the authors concluded that rivalry suppression was not tuned to orientation.

There are some important differences between our study and Nguyen, Freeman and Wenderoth (2001) that might explain the differences in results with their orientation experiment. In their study, the task for the observers was to detect the probe's location while in our experiments observers had to discriminate between probe orientations. Although this alone should not lead to different results, combined with their probe presentation technique it could have. Nguyen and colleagues added their probes to the rival stimulus using a step function that did not maintain a constant level of mean luminance. This means that detection of the probe could have been done on local luminance variations alone and thus may not have sufficed to find any specific effects of orientation on suppression. Correspondingly, their conclusions agree with previous studies using luminance probes (Blake & Camisa, 1977). In our study, mean luminance was kept constant. Moreover, our task could not be performed on luminance information alone since observers had to discriminate the probe's orientation. These differences in methods could explain why no orientation tuning was found in the Nguyen, Freeman and Wenderoth study.

The tunings implied in our suppression data are similar in bandwidth to the feature tunings observed in early visual cortex. For example, neurophysiologic estimates of orientation bandwidth in V1 from single-unit studies indicate a median half-width at half-maximum of about 21° (De Valois, Yund & Hepler, 1982). Psychophysical estimates from human observers using a variety of methods suggest very similar values (Blake & Holopigian, 1985; Govenlock, Taylor, Sekuler & Bennett, 2009). These accord well with the measurements we obtained in Experiment 1, which correspond to a half bandwidth of 26°. Similarly, estimates from neurophysiology and psychophysics indicate a full bandwidth for spatial frequency channels of between 1 and 1.5 octaves. The average bandwidth of the spatial frequency tunings plotted in Figure 5 matches this closely with a value of approximately 1 octave. Since a tight tuning to a particular feature value is a hallmark of neurons in early visual cortex, the tuned pattern of suppression we report is consistent with the specific component of rivalry suppression having an early source. Moreover, as Experiments 2 and 4 reveal, the specific, tuned component of rivalry suppression only arises when the suppressed feature is in conflict with the dominant image. In other words, there has to be 'spatial frequency rivalry' between the images for spatially-frequency tuned suppression to emerge, or 'orientation rivalry' for orientation tuning to emerge. Since visual neurons lose their feature specificity at successive stages beyond V1, this also squares with an early source for the specific component of rivalry suppression. Indeed, this component may stem from specifically targeted mutual inhibition between early feature detectors at the stage where the interocular mismatch is first detected and the rivalry process is initiated.

The specific feature tuning of suppression for conventional rivalry can be contrasted with the untuned suppression observed with flicker-and-swap rivalry in Experiment 5. Figure 6 plots suppression as a function of orientation for flicker-and-swap rivalry and compares that with the corresponding data for conventional rivalry from Experiment 1. Two major differences are evident: first, that there is no orientation tuning for flicker-and-swap rivalry, and second, that rivalry suppression overall is weaker for flicker-and-swap rivalry. The lack of feature tuning indicates that suppression in flicker-and-swap rivalry arises at a later stage than for conventional rivalry, supporting a similar conclusion from a TMS study showing that pulses over occipital cortex induced dominance switches for conventional rivalry but did not affect flicker-and-swap rivalry (Pearson et al., 2007). Together, these findings provide converging evidence that flicker-and-swap rivalry engages processes that are subsequent to those underlying conventional rivalry processes. The fact that it is unaffected by neurodisruptions by TMS in the occipital cortex and shows no orientation tuning is good evidence that it occurs after V1.

It may be tempting to conclude that the general component of rivalry suppression (the untuned baselines in Figures 2 and 5) may be the same as suppression in flicker-and-swap rivalry since both are untuned and both are weaker than the tuned portion in the conventional rivalry suppression curves. However, an important difference between these two forms of rivalry suppression is that they differ markedly in strength. This is evident when suppression strength in Figure 6 E is compared to the results of Experiments 1, 3 and 4. For all probe orientations, suppression strength for conventional rivalry is far greater than for flicker-and-swap rivalry, even in the un-tuned baseline portion for conventional rivalry. This lack of suppression strength has been reported recently by Bhardwaj et al., 2008 and it also agrees with the phenomenal experience of flicker-and-swap rivalry which often appears to produce a less convincing perceptual alternation than is experienced during conventional rivalry. Therefore, on the grounds that their respective suppression strengths differ so markedly, we do not conclude that the untuned general component of conventional rivalry can be regarded as one and the same as flicker-and-swap suppression.

In summary, our results indicate that binocular rivalry suppression is feature-dependent, with suppression strength peaking when probes are similar to the features currently suppressed in rivalry. Suppression, however, is not absent for dissimilar conflicting features but instead appears to drop off to a baseline level of suppression. Taking these findings together, we suggest that binocular rivalry suppression consists of two components, one general suppression component which is feature invariant, affecting the suppressed image as a whole and one specific component which is tuned to features in conflict and increases in strength when these conflicting features become more similar.

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Chapter 3:

Suppressed images selectively affect the dominant percept during binocular rivalry

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Abstract

During binocular rivalry, perception alternates between dissimilar images that are presented dichoptically. It has been argued that perception during the dominance phase of rivalry is unaffected by the suppressed image. Recent evidence suggests, however, that the suppressed image does affect perception of the dominant image, yet the extent and nature of this interaction remain elusive. We hypothesize that this interaction depends on the difference in feature content between the rivalling images. Here we investigate how sensitivity to probes presented in the image that is currently dominant in perception is affected by the suppressed image. Observers performed a 2AFC discrimination task on oriented probes (Experiment 1) or probes with different motion directions (Experiment 2). Our results show that performance on both orientation and motion direction discrimination was affected by the content of the suppressed image. The strength of interference depended specifically on the difference in feature content (e.g. the difference in orientation) between the probe and the suppressed image. Moreover, the pattern of interference by the suppressed image is qualitatively similar to the situation where this image and the probe are simultaneously visible. We conclude that perception during the dominance phase of rivalry is affected by a suppressed image as if it were visible.

Introduction

When incompatible images are presented to corresponding retinal locations of each eye, perception becomes unstable and alternates between the images. This phenomenon is known as binocular rivalry (Wheatstone, 1838; see Blake & Wilson, 2010 for a recent review). During rivalry, one of the images will be temporarily dominant in perception, while the other will be suppressed. Several studies on the nature of binocular rivalry suppression show that sensitivity to probes presented in the suppressed image is reduced by a factor of about 2 to 3 (Blake & Fox, 1974; Ooi & Loop, 1994; O'Shea & Crassini, 1981). Traditionally, this suppression of an image during binocular rivalry is considered to be non-selective: all inputs from the suppressed eye (i.e. the eye to which the suppressed image was presented) are thought to be uniformly affected (e.g. Fox & Check, 1966; 1968; Wales & Fox, 1970; Blake & Fox, 1974; Blake, Westendorf & Overton, 1980; Blake, 1989; Nguyen, Freeman & Wenderoth, 2001; Blake & Logothetis, 2002; Freeman, Nguyen & Alais, 2005). However, evidence that challenges this view is accumulating (Stuit, Cass, Paffen & Alais, 2009; Alais & Parker, 2006; Vergeer & van Lier, 2010; Paffen, Alais & Verstraten, 2005; O'Shea & Crassini, 1981). These latter studies argue that the magnitude of suppression during rivalry depends on the similarity in feature content between the competing images. For example, sensitivity to oriented probes presented in a suppressed image depends on the orientation difference between the probe and the suppressed image (Stuit et al., 2009). A similar dependency was shown for spatial frequency content. In addition, these studies suggest that the above dependency is only apparent for the features that *drive the interocular conflict*. For instance, variations in the magnitude of suppression for different combinations of spatial frequencies can only be found when rivalry is based on conflicting spatial frequencies of the images, not when the images have conflicting orientations with the same spatial frequency (Stuit et al., 2009). These findings show that suppression during binocular rivalry is indeed *(feature) selective*: inputs originating from a suppressed image are not necessarily affected equally.

The magnitude of suppression is not only affected by the relative difference in feature content between the rivalling images; variations in feature content within one image can influence suppression as well. Local feature differences within a single image can also alter the magnitude of suppression during rivalry (Stuit, Verstraten & Paffen, 2010; Paffen, Naber & Verstraten, 2008). That is, when a suppressed image contains multiple homogeneously oriented items and one oddball, the deviating item will reach perceptual dominance first. This bias in the origin of a perceptual alternation suggests that suppression is attenuated for regions in the suppressed image that are perceptually salient. Again, these findings indicate that binocular rivalry suppression can be selective.

While a loss of awareness for suppressed images is accompanied by a loss in sensitivity as described above, sensitivity during the dominance phase is believed to be unaffected by the presence of a suppressed rival image. Correspondingly, sensitivity to probes presented in the dominant image appears to remain largely unaffected by suppressed images (Blake & Camisa, 1979; Westendorf, 1989). Based on these results, perception during dominance has often been referred to as equivalent to non-rivalrous monocular viewing-conditions (Tsuchiya, Koch, Gilroy & Blake, 2006; Alais & Blake, 2005; Gilroy & Blake, 2004). However, in 1962, Treisman already showed that stereo depth perception can coexist with binocular rivalry. This suggests that at least some of the suppressed signals can survive rivalry suppression to alter perception during dominance. Recent findings strengthen this idea (Carlson & He, 2000; Andrews & Blakemore, 2002; Pearson & Clifford, 2005). For instance, Andrews and Blakemore (2002) showed that dichoptically presented gratings with orthogonal orientations and motion directions could combine during rivalry. Specifically, when perception alternated, the two drifting gratings often combined into a plaid with a single motion direction. Temporal frequency information has also been shown to integrate during rivalry. Carlson and He (2000) have shown that temporal luminance modulations of two competing images, having different modulation frequencies, can integrate into binocular beats (a slow flicker amplitude modulation that corresponds to the difference between the two primary frequencies), during rivalry of the images. We believe this integration can be explained by the lack of rivalry between dichoptically presented slow and fast motion signals (van de Grind, van Hof, van der Smagt & Verstraten, 2001). These findings show that part of the visual information of a suppressed image can actually escape phenomenal suppression to be part of the percept during rivalry. However, perception of part of the suppressed image (i.e. the temporal frequency or the orientation and motion signals) means the image is not completely suppressed during rivalry. Using an approach that bypasses this problem, Pearson and Clifford (2005) showed a different example of suppressed visual features altering perception during the dominance phase of binocular rivalry. In their experiment, Pearson and Clifford used rivalling gratings to show that the perceived orientation of a *dominant* grating is systematically biased by the orientation of a suppressed grating.

The magnitude of the difference between the perceived and the physical orientation, as well as the direction of this effect (a clockwise or counterclockwise shift in perceived orientation), depended on the orientation difference between the two competing images. These results suggest that a suppressed image affects the percept of a dominant image in a way that depends on the relative difference in feature content between the two images. Note that this dependence on feature content is similar to the dependence observed between feature content and the magnitude of suppression (see above).

In the current study we aim to unravel the mechanisms underlying the interaction between a suppressed image and perception of a dominant one. The suggested dependence on relative differences in feature content between two images is of particular interest. Moreover, if such a dependency is present, how does this relate to a non-rivalrous situation where suppression is not a factor and both images are simultaneously perceived?

Experiment 1

In Experiment 1 we investigated how suppressed images affect perception of dominant images during binocular rivalry. We measured sensitivity to orientated probes added to a dominant retinal image to assert the influence of suppressed visual information, referred to as the mask, on perception during rivalry dominance. This constituted our dichoptic condition. We used a baseline condition without a suppressed image to test if performance during the dominance phase of binocular rivalry differs from non-rivalrous monocular viewing. Furthermore, to test the role of the visibility of the masks, we also measured performance during a monocular condition where the test probes were directly presented onto the masks, while a flat grey image of background luminance was presented to the other eye.

Methods

Observers

Six observers, including one of the authors (SS) participated in the experiment. All had normal or corrected to normal vision and all but SS were naïve as to the purpose of the study. All observers were experienced psychophysical observers.

Apparatus

Stimuli were created on an Apple Mac Pro computer running system OS X and Matlab 7.4 with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). The stimuli were presented on a linearized LaCie III 22" at 75 Hz. Observers viewed the stimuli through a mirror stereoscope. The length of the optical path, from the eyes via the mirrors to the monitor, was 57 cm.

Stimulus and Procedure

In Experiment 1, observers performed a 2AFC orientation discrimination task on the oriented test probes presented in three different viewing-conditions (Figure 1). The test probes (1.5° of visual angle, 6.25 cpd) consisted of sine-wave gratings whose edges were smoothed with a cosine ramp of 0.32° of visual angle. The orientation of the test probes was either 5° clockwise (cw) or counterclockwise (ccw) from vertical. The presentation of the probes was self-initiated via a press of the space bar. The timing of this initiation by the observer depended on the viewing-condition (see below). After presentation of the probe, observers used the arrow keys to indicate whether the probe was oriented cw or ccw from vertical. The contrast of the probes was varied using two independent, randomly interleaved, staircases (QUEST; Watson & Pelli, 1983), both estimating the 75% correct threshold for orientation discrimination.

Using a block design, the probes were presented in different viewing-conditions: a dichoptic viewing-condition, a monocular viewing-condition and a baseline condition. In the dichoptic viewing-condition (Figure 1A), a sine wave grating, which we will refer to as the 'mask', was presented to one eye, while a spatial-frequency filtered pixel noise image was presented to the other. The masks (6.25 cpd, 98% Michelson contrast) could have one of five orientations (5, 15, 20, 45, or 90° cw relative to the probe orientation). The noise image (98% Michelson contrast) was used to initiate binocular rivalry, but also served as a pedestal for the probe. The pixel noise was band-pass filtered such that the frequency power spectrum matched that of the gratings. Both the mask and the noise image were presented within a circular aperture with a diameter of 2° of visual angle. Observers were explicitly instructed to only initiate the presentation of the probe during the dominance phase of the noise image. The observers repeated the trial if an alternation occurred during the presentation of the probe. After initiation by the observer, the probe was superimposed on the noise image. The contrast of the probe first increased and subsequently decreased along a Gaussian profile to avoid abrupt temporal onsets. The sigma of the Gaussian was 7 ms and its amplitude was chosen to match the contrast of the probe. Note that the amplitude of the Gaussian thus varied on a trial by trail basis based on the current QUEST estimate. To keep the mean luminance of the image constant, the increase in contrast of the probe was mirrored by an equal decrease in the (local) contrast of the noise image on which it was presented. The total presentation duration of the probe, from zero percent contrast to the desired probe contrast and back again, was 400 ms. This viewing-condition resulted in binocular rivalry between the grating and the noise image.

In the monocular viewing-condition (Figure 1B), the masks from the dichoptic viewing-condition were presented to one eye while a uniform gray field of average luminance was presented to the other eye. In this condition the probes were superimposed on the masks. Observers initiated the probes, via a space-bar press, when the masks were clearly visible. This viewing-condition resulted in continuous perceptual dominance of the masks and the probes.

In addition to the dichoptic and monocular viewing-conditions, we used a baseline condition (Figure 1C) in which the probe was presented in the pixel noise image, as was the case for the dichoptic condition. However, a uniform gray field of average luminance was presented to the other eye. Observers initiated presentation of the probes when the noise image was perceived. This viewing-condition also resulted in continuous perceptual dominance of the noise image and the probes.

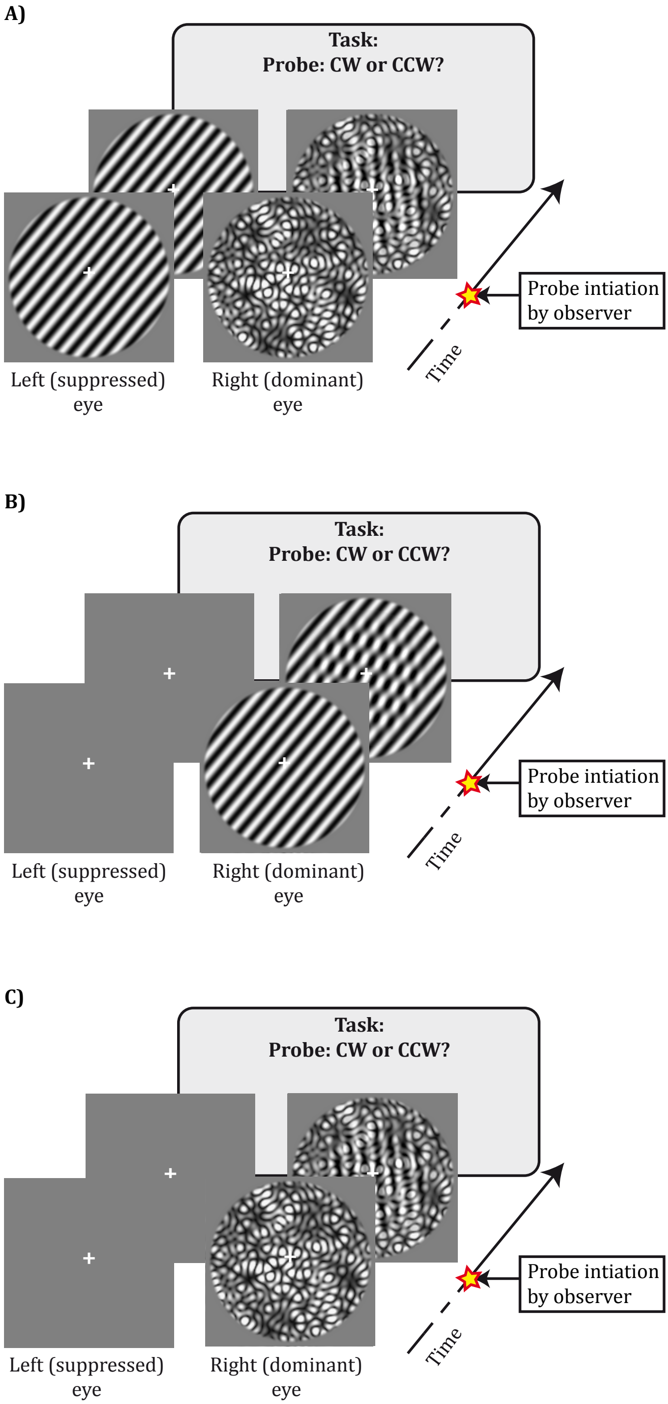
A)
Task:
Probe: CW or CCW?
Left (suppressed) eye
Right (dominant) eye
Time
Probe intiation by observer
B)
Task:
Probe: CW or CCW?
Left (suppressed) eye
Right (dominant) eye
Time
Probe intiation by observer
C)
Task:
Probe: CW or CCW?
Left (suppressed) eye
Right (dominant) eye
Time
Probe intiation by observer

Figure 1: Schematic representation of the stimulus and task for each condition of Experiment 1. A): In the dichoptic viewing-condition, a pedestal consisting of band-pass filtered pixel noise was presented to the right eye. A grating (mask) was presented to the left eye. After the observer indicated that the pedestal was perceptually dominant, a test grating (probe) was presented in the centre of the image. This grating was oriented either 5° cw or ccw from vertical. The observer's task was to indicate the orientation of the grating. B): In the monocular viewing-condition the mask was replaced with an image of background luminance. However, the pedestal was replaced with the mask. The probe was now presented in this image. C): The baseline condition also used background luminance as the left eye's image. The task and the right eye image were identical to the dichoptic viewing-condition.

Results & Discussion Experiment 1

Results for Experiment 1 are shown in Figure 2. For each observer's monocular as well as dichoptic viewing-condition, the threshold estimates from the two QUEST staircases for each mask orientation were averaged to obtain a single 75% correct threshold for probe orientation discrimination. To test whether thresholds for the monocular and dichoptic viewing-conditions were different from the baseline condition, performance was first pooled across the 5 different orientations of the mask for both the monocular and dichoptic viewing-conditions separately. This resulted in two scores reflecting performance across all mask orientations; one for dichoptic viewing and for monocular viewing. The average threshold for the dichoptic viewing-condition was significantly higher than the average of the baseline condition ($t(5) = 2.87$, $p = 0.35$). Similarly, the average threshold for the monocular viewing-condition was also higher than that of the baseline condition ($t(5) = 13.18$, $p < 0.001$). This indicates that the mask significantly interfered with discriminating the orientation of the probe, both when the mask was perceived (monocular viewing-condition) and when it was suppressed from awareness (dichoptic viewing-condition). These results show that perception during binocular rivalry dominance (dichoptic viewing-condition) is *not* the same as non-rivalrous monocular viewing (baseline condition).

Next, we compared performance in the monocular and dichoptic viewing-conditions using a 2 x 5 (viewing-condition by relative orientation) repeated measures ANOVA. The results show main effects for viewing-condition (dichoptic compared to monocular; $F(1,5) = 68.54$), $p < 0.001$) and for the relative orientation of the mask ($F(4,20) = 47.15$, $p < 0.001$) as well as an interaction between viewing-condition and relative mask

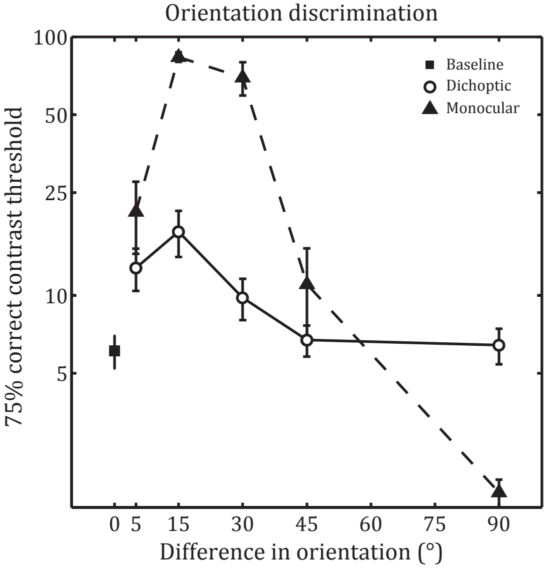

Figure 2: Results of Experiment 1. The solid line with open circles indicates the 75% correct orientation discrimination thresholds for the dichoptic viewing-condition. The dashed line with black triangles indicates the thresholds for the monocular viewing-condition. Thresholds are presented in Michelson contrast. The black square indicates average baseline performance. Error bars represent ±1 s.e.m. Note that, although the amplitudes differ, both conditions show similar effects of relative orientation. In both conditions, interference peaks at a mask orientation of ~15 degrees relative to the probe.

orientation ($F(4,20) = 29.07$), $p < 0.001$). Further comparisons based on the main effect of orientation show that both the dichoptic ($\underline{F}(4,20) = 6.831$, $p < 0.01$) and the monocular viewing-condition ($F(4,20) = 40.885$, $p < 0.001$) contain significant effects of relative orientation. This shows that under both monocular and dichoptic viewing-conditions, the effect of the mask depends on the difference between the orientation of the mask and that of the probe. For both viewing-conditions, the highest discrimination thresholds for the probes are at the 15° masks. However, based on previous results showing suppressive interactions during rivalry one can expect the peak in our distribution to be at 5° relative to the probe (Stuit et al, 2009; also see Ling, Pearson & Blake, 2009). We suggest that this is due to the spatial phase of our probes relative to that of the masks. It is known from masking studies that iso-oriented masks that are in-phase can facilitate probe detection (Georgeson & Georgeson, 1987). Indeed, our masks and probes were in-phase. The correspondence to these lower thresholds in our results and effects found in masking studies strengthens previous suggestions that binocular rivalry and masking involve a common suppressive process (Baker & Graf, 2009).

The pattern of dependency on relative orientation difference between the probes and masks was similar for both conditions. However, all thresholds, except for the 90° masks, were larger in the monocular viewing-condition (see Figure 2). The interaction between viewing-condition and the relative orientation of the mask reflects the lower threshold for the 90° mask in the monocular viewing-condition in combination with all other thresholds being higher. We suggest the lower threshold for 90° mask is due to centre-surround interactions. For orthogonal orientations, centre-surround interaction can result in facilitation to the centre (Gilbert & Wiesel, 1990; Cass & Spehar, 2005). However, this effect is not observed in the dichoptic condition. We suggest this is because the surrounds were suppressed during the presentation of the probes and weaker surrounds result in weaker centre-surround interactions (Snowden & Hammett, 1998). In conclusion, our results indicate that perception during binocular rivalry dominance (dichoptic viewing-condition) depends on the content of the suppressed image. The suppressed image therefore has a selective influence on sensitivity to the dominant image.

Experiment 2

In Experiment 1 we observed interactions in both the dichoptic and monocular viewing-conditions, based on the orientation of the mask relative to the probe. Although this is in accordance with our hypothesis, stating that the difference in feature content modulates the degree to which suppressed and dominant images interact during binocular rivalry, this interaction may be limited to *orientation* information. To test the possibility that other features show similar interactions during rivalry, we set out to extend the findings of Experiment 1 using a different feature: *global motion direction*. The main reason for this choice is the assumed dependency on visual areas more upstream in the visual system compared to orientation processing (Shiller, Finlay & Volman, 1976; Albright, 1984). In Experiment 2 we measured the influence of masks containing a range of different motion directions, on motion direction discrimination of the probe. As in Experiment 1, the masks and probes could be presented either monocularly or dichoptically.

Methods

Observers

Six observers, including one of the authors (SS) and 2 observers from Experiment 1, participated in the experiment. All had normal or corrected to normal vision and except for SS, were naïve to the purpose of the study.

Apparatus

The experimental setup was the same as for Experiment 1, except that the refresh rate of the monitor was increased to 85 Hz to facilitate the percept of smooth motion.

Stimulus & Procedure

In Experiment 2, observers performed a 2AFC motion direction discrimination task under three different viewing-conditions (Figure 3). The probes in this experiment consisted of white noise images in which the noise was moving either left- or rightwards at a velocity of 1.13°/sec. To obtain the 75% correct threshold for motion direction discrimination, the contrast of the probes was varied using adaptive staircases for each mask direction (QUEST; Watson & Pelli, 1983). Each threshold was estimated twice using independent, randomly interleaved, staircases. As in Experiment 1, presentation of the probes was self-initiated using a space bar press after which observers indicated (in a 2AFC design) whether the motion in the probe was to the left or to the right using the arrow keys.

As in Experiment 1, we had three viewing-conditions: dichoptic, monocular and a baseline condition. In the dichoptic viewing-condition a mask was presented to one eye while the pedestal for the probe was presented to the other eye (Figure 3A). The masks consisted of white noise images in which the noise moved linearly in one of several possible directions. The speed in the masks was identical to that in the probes. The difference in motion direction between mask and probe was varied from 15° to 165°, in 15° steps. The mask was always presented at 7.2% RMS contrast. The relatively low contrast for the masks, compared to Experiment 1, was chosen to counter the strong tendency for linear motion signals to be dominant during rivalry (as seen in a pilot version of the experiment). We did not expect any difference in using low-contrast compared to high contrasts masks since performance on global-motion performance saturates at relatively low contrasts (Müller & Greenlee, 1994; Edwards, Badcock &

Nishida, 1996). For the pedestal, which was used for the superimposition of the probes as well as to instigate binocular rivalry, we again used a white noise image (29% RMS contrast). The noise in the pedestal, however, rotated at .24 revolutions per second. The rotation direction was randomized and could be either cw or ccw. To avoid abrupt onsets, the probes were superimposed on the pedestal using a temporal Gaussian profile. This means the probe contrast first increased and subsequently decreased over time. The sigma of the Gaussian was 8 ms and the amplitude corresponded to the contrast of the probe. Note that the amplitude thus varied per trial based on the current QUEST threshold estimate. To keep the average luminance of the image constant, the increase in contrast of the probe was mirrored by an equal decrease in the (local) contrast of the image on which it was presented. The total presentation duration of the probe, from zero percent contrast to the desired probe contrast and back to zero, was 258 ms. During the dichoptic viewing-condition, observers waited for the dominance phase of the pedestal before they initiated the presentation of the probe. Observers were instructed to repeat the trial in case an alternation occurred during presentation of the probe. This viewing-condition resulted in binocular rivalry of the competing noise images.

In the monocular viewing-condition (Figure 3B), the probes were superimposed on a combination of the pedestal and masks used in the dichoptic viewing-condition. This combination was created using the alpha blending functions of the Psychophysics Toolbox, which kept the contrast ratio of the images the same as in the dichoptic viewing-condition. This combined image was presented to one eye while a uniform gray field of average luminance was presented to the other. We chose to combine the mask and pedestal into a single image since the contrast of the mask was only 7.2% RMS in this experiment. Superimposing the probes onto the masks as in Experiment 1 would result in different contrast-based signal to noise ratios of the probe and pedestal between the two viewing-conditions. More specifically, the signal to noise ratio of the probe would be almost four times greater in the monocular viewing-condition compared to the dichoptic viewing-condition. This would make the comparison between the two viewing-conditions very difficult. Note that this viewing-condition resulted in continuous perceptual dominance of the mask-pedestal combination onto which the probes were presented.

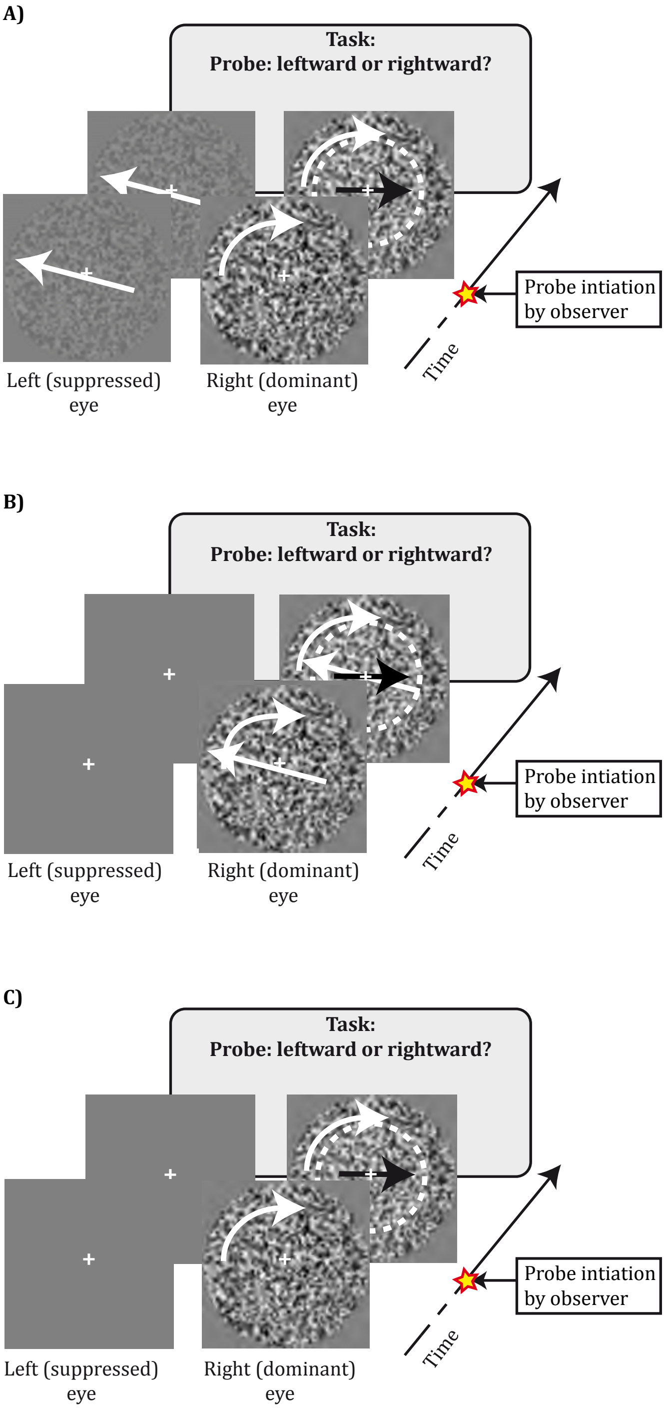
A)
Task:
Probe: leftward or rightward?
Probe intiation by observer
Time
Left (suppressed) eye
Right (dominant) eye
B)
Task:
Probe: leftward or rightward?
Probe intiation by observer
Time
Left (suppressed) eye
Right (dominant) eye
C)
Task:
Probe: leftward or rightward?
Probe intiation by observer
Time
Left (suppressed) eye
Right (dominant) eye

Figure 3: Schematic representation of the stimulus and task for each condition of Experiment 2. The arrows indicate one of the possible directions of motion. A): In the dichoptic viewing-condition the pedestal consisted of an image of rotating white noise and was presented to the right eye. The rotation direction could be either cw or ccw. A pixel noise image (mask) was presented to the left eye. After the observer indicated that the rotating noise image was perceptually dominant, a probe was presented in the centre of the image, as indicated by the dotted white circle. The probe contained either leftward or rightward moving noise. The observer's task was to indicate the direction of motion in the probe. B): In the monocular viewing-condition the left eye's image was background luminance only. The right eye's image consisted of a combination of the mask and the rotating noise image. C): In the baseline condition the right eye's image was the same as in the dichoptic viewing-condition. An image of background luminance was presented to the left eye.

As in Experiment 1, we also used a baseline condition in which no mask was presented (figure 3C). The probe was presented on the rotating white noise only, just as in the dichoptic condition. However, here a uniform gray field of average luminance was presented to the other eye. This viewing-condition resulted in continuous perceptual dominance of the white noise image onto which the probes were presented.

Results & Discussion Experiment 2

Results for experiment 2 are displayed in Figure 4. For each observer the two threshold estimates for each mask direction from the monocular as well as dichoptic viewing-conditions were averaged to obtain a single threshold for motion discrimination. We first tested whether performance during the monocular and dichoptic viewing-conditions was different from the baseline condition. For this, the threshold estimates for all mask-directions of both viewing-conditions were first pooled separately. The averages of the pooled estimates were subsequently compared to the baseline performance. Unlike the results of Experiment 1, the dichoptic and monocular viewing-conditions did not differ from the baseline condition (dichoptic: $t(5) = 0.133$, $p = 0.899$; monocular: $t(5) = 0.908$, $p = 0.405$). However, inspection of Figure 4 suggests that the effect of the masks might be limited to the probe-mask combinations with the greatest difference in direction. To test whether direction discrimination performance of the probes is differentially affected by the direction of the mask, we used a 2 x 11 (viewing-condition by relative motion direction) repeated measures ANOVA to test for a dependency on (relative) motion direction of the mask. The analysis revealed a significant main effect of direction

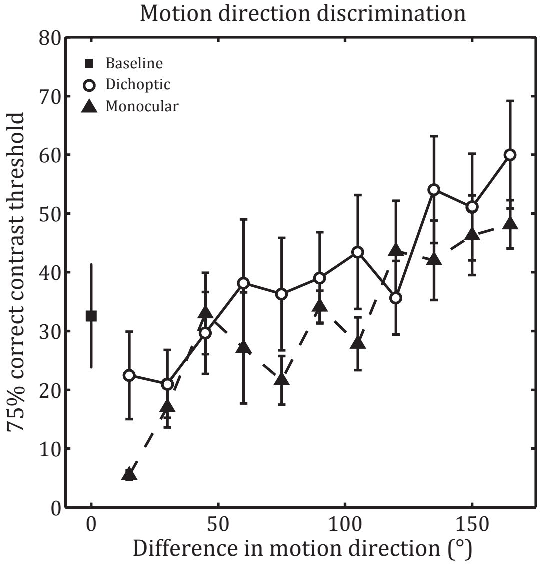

Figure 4: Results of Experiment 2. The solid line with open circles indicates the average 75% correct motion direction discrimination thresholds for the dichoptic condition; the dashed line with the black triangles shows the average thresholds for the monocular condition. The black square indicates the average threshold of the baseline condition. Thresholds are represented in RMS contrast. Error bars represent ± 1 standard error of the mean. These results show the dependency on the difference in motion direction between mask and probe for both the monocular and dichoptic condition. Also note that the thresholds are similar for the different conditions.

($F(10,50) = 6.78$, $p < 0.001$). Interestingly, we found no difference between the viewing-conditions (dichoptic vs. monocular; $F(1,5) = 1.573$, $p = 0.265$) and no interaction between mask direction and viewing-condition ($F(10,50) = 0.84$, $p = 0.590$). These results show that the masks affected probe discrimination similarly across viewing-conditions, irrespective of whether the mask was dominant in perception or not.

Interestingly, the pattern of results differs from that of Experiment 1. In that experiment the magnitude of the orientation effect differed between viewing conditions. The discrepancy in effect-sizes for orientation (dichoptic mask effect differs from the monocular mask effect) and motion direction (no difference in masking effects between the dichoptic and monocular viewing-conditions) may be explained by a difference in methods between the monocular viewing-conditions of the experiments. In Experiment 1 we used the masks from the dichoptic viewing-condition as the pedestal for the monocular viewing-condition. This means that the interfering orientation signals were stronger in the monocular viewing-condition, compared to the dichoptic, since they were not suppressed from awareness. However, in the monocular viewing-condition of Experiment 2, we used a combination of the mask and the noise image as the pedestal. Here, the strengths of the interfering motion signals were the same for both the monocular and dichoptic viewing-conditions. The relatively greater strength of the orientation masks (for monocular compared to dichoptic, in Experiment 1) may explain why the probe discrimination thresholds were higher in the monocular compared to the dichoptic viewing-condition. To test this possibility, we ran a control experiment in which we combined the oriented mask and noise image in the same manner as Experiment 2. Three observers from the original experiment completed the 15°, 30° and 45° (relative to the probe) mask conditions. We found no difference between the control and the original monocular condition (mean thresholds for original 15°, 30° and 45° conditions: 84.96, 62.64 and 7.96 respectively; mean thresholds for control 15°, 30° and 45° conditions: 92.32, 66.18 and 13.10 respectively; $F(1,2) = 0.461$, $p = 0.567$), nor did we find any interaction between the version of the experiment (original or control) and relative orientation (15°, 30° or 45°; $F(2,4) = 0.064$, $p = 0.939$). This shows the composition of the pedestal cannot explain the larger orientation effects in the monocular compared to the dichoptic viewing-condition.

General Discussion

In this study we investigated the interactions between suppressed and dominant images when engaged in binocular rivalry. We measured sensitivity to both orientation probes and motion direction probes added to a dominant retinal image to assert the influence of suppressed visual information on perception during rivalry dominance. The results show that, in contrast with a long-standing belief, perception during the dominance phase of binocular rivalry *is* affected by the suppressed image. Moreover, we show that, for features like orientation and motion direction, the effect exerted by suppressed images on perception during dominance depends on the difference in feature content (e.g. orientation difference) between the rivalling images. The nature of the interaction was the same during non-rival viewing-conditions. This suggests that an image, which is suppressed from awareness, affects a perceptually dominant image *as if* it were actually visible.

For rivalling orientations rivalling and motion directions, the amount by which a suppressed image affects perception during dominance depends on the relative differences between the two images. The dependency on these relative differences suggests a general role for feature interactions in binocular rivalry. This suggestion is in line with previous suggestions based on exclusivity during rivalry (Knapen et al., 2007) as well as the strength of rivalry suppression (Stuit et al., 2009). For instance, orientation discrimination performed on test probes during the suppression phase shows a similar dependency on the relative orientation difference between the probe and the suppressed image as found in the current study (Stuit et al., 2009). Thus, an image that is suppressed during rivalry affects probes presented during dominance similarly as those presented during suppression.

At first sight, a possible explanation for the results of Experiment 1 is adaptation to the mask's orientation. Some adaptation effects have been shown to persist even when an image is suppressed from awareness (see Blake & He, 2005 for a review). Although some adaptation is likely to have occurred, our methods exclude adaptation as a causal factor. More specifically, adaptation to the mask-orientation would affect both the clockwise- and counterclockwise probes in the same manner within each mask condition with either attraction or repulsion (e.g. leading to a tilt after effect). This is because the masks were always presented cw relative to the probes. Adaptation to the masks would then result in one of the probes being perceived more tilted *towards* vertical (e.g. more difficult to discriminate from vertical), while the other probe is perceived as tilted more *away* from vertical (e.g. less difficult to discriminate from vertical). Since the orientation of the probe was counterbalanced, any adaptation effects would be averaged out of the discrimination thresholds. Although this does not mean there was no adaptation to the different mask-orientations in the experiment, it does imply that the pattern in our results is not caused by adaptation. Note that adaptation can't be considered as a causal factor in Experiment 2 since the pattern of direction dependency is opposite to what is expected for adaptation: Masks with similar directions to the probe do not interfere with probe direction discrimination.

Previous looks at interactions between images competing for awareness during rivalry have shown only modest effects. Pearson and Clifford (2005) showed that the effect of a suppressed grating on the percept of a dominant grating during rivalry is reduced approximately by a factor of 6, in comparison to the condition in which the suppressed grating was simultaneously perceived. We found a similar reduction in Experiment 1. However, in Experiment 2, the effect of the masks on motion discrimination was similar in terms of magnitude for both dichoptic and monocular viewing-conditions. This shows that the reduction in effect-size due to suppression does not hold for all features. Instead, the different effect-sizes demonstrate that orientation signals exert less influence on perception during dominance than motion signals.

The above is likely to be due to the difference in the loci of processing of orientation and motion direction stimuli. Compared to other areas, V1 has the greatest percentage of orientation selective neurons (Shiller, Finlay & Volman, 1976), whereas area MT has the largest percentage of direction selective neurons (e.g. Albright, 1984; Snowden, 1994). While the majority of orientation selective neurons in V1 exhibit at least some eye-preference (e.g. Hubel & Wiesel, 1962), the direction selective neurons in MT receive exclusive binocular inputs (e.g. Rodman, Gross & Albright, 1989). If we take these different properties of areas V1 and MT into account, the neurons responsive to our stimuli in Experiment 1 were only partly overlapping between the monocular and dichoptic viewing-conditions, resulting in different effect-sizes for the two conditions. However, the same neurons might have been involved in both the monocular and dichoptic viewing-conditions of Experiment 2. Hence, the similar results observed there. It is generally acknowledged that rivalry competition can occur at multiple stages of the visual processing hierarchy (Blake & Logothetis, 2002; Nguyen, Freeman, & Alais, 2003; Lee, 2004; Freeman, 2005; Silver & Logothetis, 2007). The occurrence of rivalry competition at different stages for motion direction and orientation stimuli is then relevant when one tries to explain the differences in the magnitude of interference between the monocular and dichoptic viewing conditions.

The assumption of different loci also concurs with the difference in interference patterns of the two experiments. In area V1, neighbouring neurons with *similar* orientation tuning inhibit each other (De Valois, Yund & Helper, 1982). This property is reflected in the results of Experiment 1 where we found greater interference of *similar* orientations compared to orthogonal orientations (Figure 2). Although V1 shows direction-selectivity, this area does not seem to exhibit directional opponency (Snowden, Treue, Erickson & Anderson, 1991). Also, V1 is less sensitive to global motion compared to MT (Braddick, O'Brien, Wattum-Bell, Atkinson & Turner, 2000), limiting its involvement in the direction dependent effects seen in the results of Experiment 2. In contrast to V1, area MT does exhibit directional suppression: neurons with *opposite* preferred directions inhibit each other (Braddick, O'Brien, Wattum-Bell, Atkinson, Hartley & Turner, 2001; Snowden, Treue, Erickson & Anderson, 1991). Correspondingly, in Experiment 2 we find the greatest interference by the masks containing a motion direction that is near *opposite* to that of the probe (Figure 4). The difference of the patterns of interference between the orientation and motion direction masks thus appears to result from their difference in processing loci.

In conclusion, in contrast to long-standing beliefs, our results show that perception during binocular rivalry dominance is affected by the nature of, and the difference between, the features present in the competing images. This influence of the suppressed image is bi-directional: sensitivity during dominance is similarly affected by the suppressed image as sensitivity during suppression. Moreover, our results show that the suppressed image affects perception during dominance as if it were actually visible.

Chapter 4:

Saliency in a suppressed image affects the spatial origin of perceptual alternations during binocular rivalry

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Abstract

During binocular rivalry, perception alternates between dichoptically presented incompatible images. With larger images, such perceptual alternations will typically start locally and then gradually spread across the image, known as travelling waves of perceptual dominance. Several image-features (such as local contrast) are known to determine where in the image a travelling wave originates. Here we investigate whether orientation contrast in the suppressed image affects these spatial origin(s) of perceptual alternations. The results show that the origins are increasingly biased towards locations of increasing orientation contrast in the suppressed image. This increase in bias is related to the efficiency of visual search for the orientation contrast, tested offline: we find large biases towards orientation contrast when visual search for it is efficient, and small biases when search for it is inefficient. Our results imply that rivalry suppression is not homogenous across the suppressed image, but is dependent on local image-features in the suppressed image. The relation between spatial bias and visual search performance suggests that spatial origins of perceptual alternations are biased to salient locations in the suppressed image. Moreover, the finding that saliency affects the spatial origin of a perceptual alternation is in agreement with the idea that saliency is represented at a monocular, unconscious level of visual processing.

Introduction

When two interpretations of the visual world are equally likely, perception becomes bistable and will alternate between the two interpretations (e.g. when viewing a Necker cube). Likewise, when dissimilar images are presented to corresponding retinal locations, perception will also alternate. This phenomenon is known as binocular rivalry (for recent reviews see: Alais & Blake, 2005; Tong, Meng & Blake, 2006). During binocular rivalry, one image will be *perceptually dominant*, while the other image is phenomenally invisible, referred to as *perceptually suppressed*. Perception will alternate between the two images in a stochastic manner, with the dominance of one image lasting a few seconds at a time (Lehky, 1995).

With the exception of small stimuli, in which alternations occur in an all-or-none fashion (Blake, O'Shea & Mueller, 1992), perceptual alternations during binocular rivalry typically start at isolated locations and continue in a gradual, wave-like fashion termed *travelling waves of perceptual dominance* (Wilson, Blake & Lee, 2001). Recently, it was shown that both the direction (Knapen, van Ee & Blake, 2007; Maruya & Blake, 2009) and speed (Naber, Carter & Verstraten, 2009) of travelling waves is dependent on characteristics of the suppressed image. However, it is still an outstanding question what determines the spatial origins of such travelling waves.

There are two known factors that determine where a travelling wave starts. The first refers to a sudden contrast increment. A brief contrast increment in the suppressed image triggers a travelling wave at that position (Wilson, Blake & Lee, 2001; Lee, Blake & Heeger, 2005; 2007). This method was adapted from studies showing that abrupt contrast increments in suppressed images can induce perceptual alternations (Blake & Fox, 1974; Mueller & Blake, 1989). The second factor concerns local differences within image features. Looking at the role of local image parameters, Paffen, Naber and Verstraten (2008) showed that perceptual alternations most often originate at those locations where luminance contrast or motion speed were higher, or spatial frequency was lower, in the suppressed image compared to the dominant image. From these observations it is clear that a variety of local image characteristics can affect the spatial origins of perceptual alternations. Although it is a possibility that these different image characteristics all affect perceptual alternations independently, a common principle would provide a more parsimonious explanation. Here we hypothesize that local saliency in the suppressed image is the common denominator responsible for determining the spatial origin of a perceptual alternation. That is, we argue that perceptual alternations will most likely originate at the location of highest saliency in the suppressed image. This hypothesis is based on the fact that all stimulus properties effective in determining the spatial origin of a perceptual alternation (abrupt contrast pulse, high contrast etcetera) are marked by high relative saliency (higher compared to the rest of the suppressed image). Since the term saliency is quite nebulous and is used in many different contexts, we will use it here when referring to the degree to which an item stands out from its surroundings (e.g. Itti & Koch, 2000; Yantis, 2005). Our hypothesis makes a strong prediction: if the origins of perceptual alternations are biased towards salient locations within a suppressed image, the origins of perceptual alternations will be biased towards an item that stands out from its surroundings even when the observer is unaware of its location.

In the current study we aim at manipulating visual salience by varying orientation contrast within an image (see Figure 1). There are good reasons for using orientation contrast to manipulate salience. For one, using orientation contrast allows us to vary saliency - the degree to which an item stands out from its surroundings - in a controlled fashion. In addition, it is generally acknowledged that visual saliency of a deviant orientation relies on centre-surround interactions at the neural level (Itti & Koch, 2000; Nothdurft, 2000). Centre-surround interactions refer to the modulation of a neuron's response by stimulation of its non-classical receptive field. Specifically, visual neurons can be excited by stimulating their classical receptive fields (CRF) with their preferred stimulus (e.g. their preferred orientation, Hubel & Wiesel, 1968) and stimulation adjacent to the CRF does not by itself elicit a response. However, stimulation of the area adjacent to the CRF (the non-classical receptive field (nCRF)) *can* modulate the response when the CRF is simultaneously stimulated (e.g. Blakemore & Tobin, 1972). For instance, for orientation-selective cells, the degree of modulation is dependent on the difference between the orientations presented to the CRF and its surround. When both are the same, the cell's response is maximally suppressed (iso-feature suppression; Cannon & Fullenkamp, 1991; Sillito, Grieve, Jones, Cudeiro & Davis, 1995; Levitt & Lund, 1997); when the orientations are orthogonal, suppression by the nCRF is minimal, or can even change to excitation (Gilbert & Wiesel, 1990; Gilbert, Ito, Kapadia & Westheimer, 2000). Importantly, these centre-surround interactions are suggested to be responsible for an item with an orthogonal orientation (as in Figure 1) to pop-out from a display (i.e.

to be salient), perhaps by increasing effective contrast of that item (Itti & Koch, 2000; Nothdurft, 2000; Yu, Klein & Levi, 2001).

Below, we show that the spatial origins of perceptual alternations are biased towards the location containing orientation contrast in the suppressed image. Next, we vary the amount of orientation contrast parametrically. In addition, we assess the degree of visual saliency for different orientation contrasts in a visual search paradigm. We show that the degree of orientation contrast is related to the degree to which alternations are biased towards locations containing the contrast: locations containing maximum orientation contrasts lead to strong biases towards these locations, whereas locations of low orientation contrast lead to small biases. Interestingly, the amount of bias towards a location containing orientation contrast appears to be more closely related to efficiency of visual search: locations with orientation contrasts that lead to efficient search lead to large biases towards these locations; locations with orientation contrasts leading to inefficient search lead to small biases.

Experiment 1

The goal of Experiment 1 is to determine whether the starting point of a perceptual alternation is biased towards the location of greatest orientation contrast in a suppressed image. To avoid any voluntary attentional effects prior to a perceptual alternation, observers should be unaware of the presence or absence of a location of high orientation contrast in the suppressed image and, when present, should also be unaware of its location. To satisfy this prerequisite, the luminance contrast of the image in which orientation contrast was manipulated (Figure 1) was gradually increased from 0 % to the point that the strength of the image was sufficient to start a perceptual alternation (see Figure 2). When such an alternation started, the observer’s task was to report *where* in the image it started.

Methods

Observers
A total of 8 observers, including two of the authors (ss and cp), took part in the experiment. All had normal or corrected to normal visual acuity and all, except ss and cp, were naïve as to the purpose of this study. All observers were experienced psychophysical observers and used to performing in experiments dealing with binocular rivalry.

Apparatus
All stimuli were created using an Apple G5 computer running system OS X and Matlab 7.4 with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). The stimuli were presented on a linearized LaCie III 22" at 75 Hz. Observers viewed the stimuli through a mirror stereoscope. The viewing distance, from the eyes via the mirrors to the monitor, was 57 cm.

Stimuli
The stimulus consisted of two images of 169 Gabors aligned on a grid of 6.3 by 6.3° of visual angle (Figure 1). The background was gray (29.9 cd/m^2). All Gabors had a spatial frequency of 6 cpd, a sigma of 0.16° and were presented with a peak contrast of 99.5% Michelson (space-average luminance: 29.9 cd/m^2; Fredericksen, Bex & Verstraten, 1997). The inter-element distance, measured centre to centre, was 0.52° of visual angle. For one of the images, which we label *the suppressor*, all Gabors were oriented vertically. For the other image, *the test-image*, the Gabors were oriented obliquely (for 50% of the trials, the orientation was clockwise, for the other 50% counterclockwise). For 50% of the trials (*probe present* trials), local orientation contrast was manipulated in the test-image by orienting one of the Gabors orthogonally to its neighbours. This deviant Gabor - *the probe* - was presented to either the upper left, upper right, lower left or lower right of the test-image's centre (presentation at each location was balanced). The distance between the probe and the fixation cross was always 3.7°. Note that for all Gabors in the test-image, including the probe, the interocular orientation difference with the suppressor was held constant at 45°. Thus, the amount of local conflict between the rival images was held constant across the image. Binocular fusion was aided by presenting a white border around the images and a white fixation cross (0.44 x 0.44°) at the centre of the display.

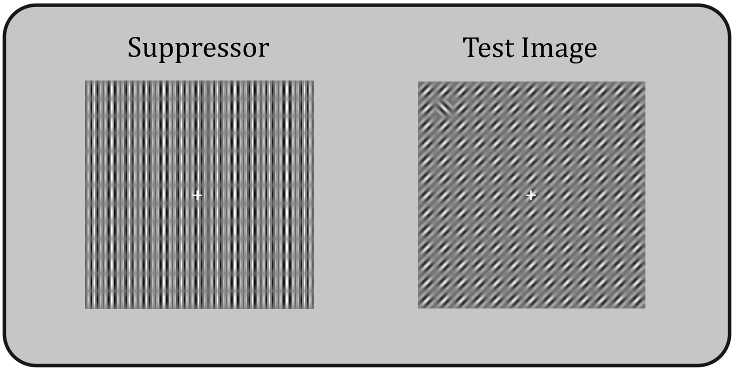


Figure 1:
The stimulus used in Experiment 1. The image on the left of Figure 1 depicts the suppressor. The image on the right displays an example of a test-image containing a probe in the upper left corner. Note that the orientation difference between a Gabor in the suppressor and a Gabor at the corresponding location of the test-image is 45° for all locations. The amount of local interocular conflict was thus constant across the image.

Procedure

At the start of each trial, the suppressor was presented at full contrast, while the contrast of the test-image was gradually increased from 0 to 100% contrast over a period of 10.6 s. The result of this procedure was that, at the start of a trial, the suppressor image was perceptually dominant, and the test-image invisible, making the presence and location of the probe unknown to the observer. The observer's task was to press a key as soon as the test image (consisting of oblique orientations) became visible. The key press triggered the removal of the rival images, leaving only the fixation cross and the borders originally surrounding the images. After the removal of the images, the cursor became visible at the location of the fixation cross in the stimulus area previously containing the test-image. Observers were instructed to move the cursor to the location at which the alternation originated and click the mouse button at that location. Presentation of the test-image and the suppressor was counter-balanced between the eyes. A schematic representation of the procedure is presented in Figure 2. Each observer completed 320 trials; 40 trials for each probe location and 160 trials without any probes presented.

Schematic Representation of a Single Trial

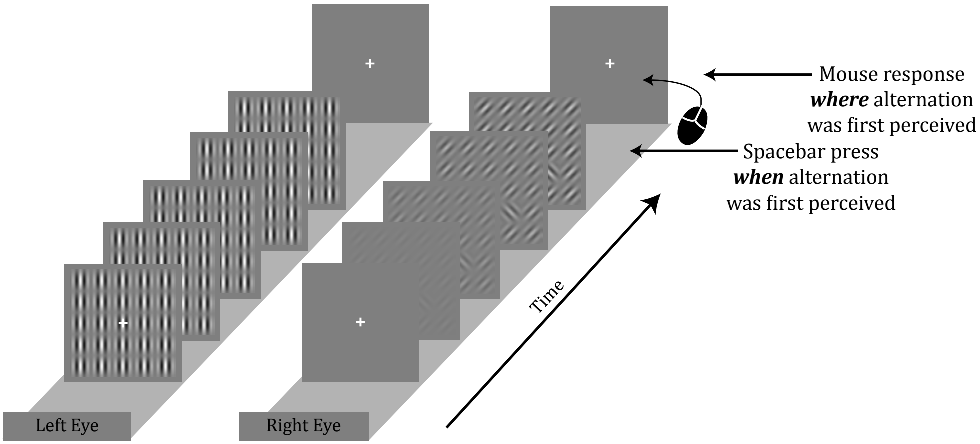


Figure 2:
A schematic representation of a single trial with schematic representations of the stimulus. In this trial the suppressor is presented to the left eye and the test-image, containing a probe in the lower right corner, to the right eye. The suppressor starts at 100% contrast while the test-image starts at 0% contrast, and subsequently increases its contrast over time. As soon as observers noticed a diagonal Gabor they responded with a space-key press. Next, both Gabor arrays were removed from the screen and observers indicated with a mouse click where they first perceived a diagonal Gabor.

Results

To analyze the spatial origins of perceptual alternations, we first converted the coordinates of the mouse clicks into 2-dimensional matrices, equal in size to the test-image, representing the spatial locations of the clicks (for details of this procedure, see Paffen et al., 2008). This resulted in 5 matrices for each observer: one for each of the 4 probe locations (i.e. *probe present* trials) and one for the *probe absent* trials. One such matrix contained all the reported origins of perceptual alternations for that condition (say probe present in left upper corner). The 4 matrices representing the data of *probe present* trials were subsequently rotated 0, 90, 180 or 270° depending on the original probe location. After rotation, the data in these 4 matrices were always relative to a probe in the upper left corner of the image. For each observer these 4 matrices were summed to create one matrix representing all responses on *probe present* trials, with all responses relative to the same probe (the upper left) location. This matrix was convolved with a two-dimensional Gaussian with an amplitude of 1 and a sigma of 0.26°. This sigma corresponds to half the inter-element distance. The peaks in these distributions now represent locations that were most frequently indicated as the spatial origin of the perceptual alternations.

We adapted our procedure for trials that did not contain probes so that we could compare the distributions of perceived origins of perceptual alternations with and without a probe in the suppressed image. The distribution of responses in *probe absent* trials reveals biases in spatial origins of perceptual alternations unrelated to locations containing orientation contrast in the suppressed image. Since these biases were likely to be present in *probe present* trials as well, and since rotating the matrices containing the data of these trials displaced the locations of these biases, we also rotated the matrices of responses for the *probe absent* trials. For each observer, the data point of each *probe absent* trial was assigned to one of four bins. The data of the four bins were rotated either 0, 90, 180 or 270°, summed, and convolved with the same Gaussian as used for the *probe present* trials. This procedure of binning and convoluting data for *probe absent* trials was repeated 100 times per observer. The final distribution was acquired by taking the mean of the 100 distributions.

To test whether spatial origins of perceptual alternations were biased towards the location of greatest orientation contrast in the suppressed image, we converted our

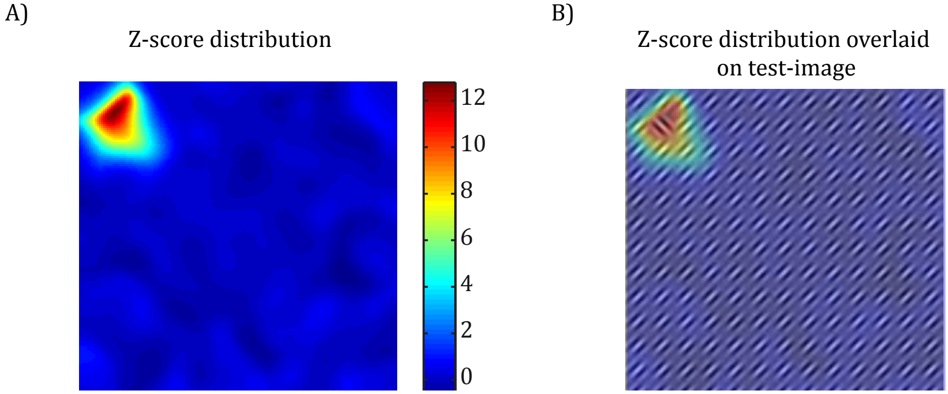


Figure 3:

Figure 3A depicts the averaged spatial distribution of responses, indicating perceived spatial origins of the perceptual alternations, converted to Z-scores. Note that all Z-scores are made relative to a probe in the upper left corner. To illustrate this more clearly, the distribution of Z-scores is overlaid on the test-image in 3B. Note the high z-scores in the distribution on the location of the probe.

data to Z-scores. We took the means across observers of the *probe present* data and the *probe absent* data. This resulted in two matrices representing the mean distributions of indicated origins of perceptual alternations of the *probe present* and *probe absent* data. We subsequently subtracted the mean *probe absent* matrix from the mean *probe present* matrix and dividing that number by the standard deviation of the *probe absent* matrices across observers (Figure 3). The alpha was set at 0.05 and corrected for spatial dependence of the data by applying the Expected Euler Characteristic as used in Random Field Theory (Adler, 1981). By using the expected Euler Characteristic we take into account the dependence of each data point to the surrounding data. Using this approach, our alpha was corrected to ~0.000067, corresponding to Z-score of 3.82. Figure 3 shows that the highest peak in this Z-score landscape (12.79) closely corresponds to the location of the probe in the suppressed image. Note that this Z-score is far above the Z-score needed for a significant bias. This shows that the spatial origins of perceptual alternations were significantly biased towards the location with the orientation contrast in the suppressed image.

Probe orientation	Upper Left Quadrant		Upper Right Quadrant		Lower Left Quadrant		Lower Right Quadrant	
0°	1.73 %	22.40%	2.26%	30.90%	1.39%	23.44%	1.39%	16.49%
5°	2.43%	22.40%	1.74%	24.65%	1.56%	22.05%	2.95%	22.22%
10°	5.73%	24.48%	2.60%	22.05%	2.60%	21.18%	1.39%	19.97%
20°	9.55%	23.78%	3.30%	18.58%	2.08%	20.49%	2.26%	19.97%
45°	11.11%	20.49%	2.26%	20.49%	2.26%	18.58%	2.08%	22.74%
90°	11.91%	22.40%	2.60%	19.97%	1.22%	21.35%	1.91%	18.75%

☐ Probe area

░ Potential probe area

▓ Non probe area

Table 1:
Table 1 presents the average percentage of responses indicating perceived locations of alternations per image-quadrant for probe absent and probe present trials. The percentages of responses are further subdivided into responses falling within the probe area (for the upper left quadrant) or potential probe area (for the other quadrants) and the regions outside the (potential) probe area. This (potential) probe-area for each quadrant is an area of .8° visual angle centred on the probe location (for the upper left quadrant) or the areas where a probe could have been presented (the potential probe areas). Note that the presented trials are rotated such that all probes fall in the upper left quadrant. Correspondingly, we see a strong increase in response in the upper left quadrant's probe area.

The matrixes containing the mean indicated origins were further divided into 8 regions (see Table 1). The data were first divided into 4 quadrants, each of which was subsequently divided into 2 areas; a (potential) probe area and a non-probe area. The (potential) probe-area for each quadrant is a circular area of 0.8° of visual angle centred on the probe location (for the upper left quadrant) or the areas where a probe could have been presented (for the other 3 quadrants). The size of this area was chosen to encompass the entire probe as well as a small part of its surround to correct for the lack of precision in indicating the location of a perceptual alternation. The non-probe area responses refer to the responses in the residual area within each quadrant after excluding the (potential) probe-area. This subdivision allows us to quantify the bias towards the potential probe areas. Since the probes were only presented at one of four possible locations, observers might recognize this and may be more likely to indicate these locations. This potential bias was quantified by dividing the average percentage of responses of the potential probe areas of the probe absent trials by the average percentage of responses to an area of similar size of the non-probe areas of the probe absent trails. The result of this indicates that, even though the probe was absent, a potential probe area was 5.9 times more likely to be indicated compared to an area of similar size in the non-probe area. However, when a probe was present, this ratio increased to 51.5 (ratio of responses in probe area to area of similar size in non-probe area). The percentages are reported in Table 1. Thus, although there was some bias to report possible probe locations (see the percentage responses to possible probe areas in probe absent trials) in the absence of a probe, presenting an invisible probe resulted in much higher biases to report the location of the probe as the origin of the perceptual alternation.

The lack of awareness of the probes was tested separately in a control experiment. For this task we used the same stimulus configurations as in Experiment 1. However, now there were only probe-present trials (160) and the stimulus was removed from the screen after a fixed duration. For each observer, this duration was his or her mean time until a perceptual alternation (as measured in Experiment 1) minus one standard deviation of this mean (mean and standard deviations used for the four observers: 2.04±0.39(s); 2.29±0.96(s); 3.69±1.52(s); 3.60±1.94(s)). The task for the observer was a 4AFC task to indicate in which quadrant the probe was being presented. Results indicated that performance was at chance level with a mean of 26.1% (95% confidence interval: 22.7-29.5%). These results provide evidence for our claim that just before an alternation started, the probe was invisible.

Experiment 2

From the results of Experiment 1 it is evident that the spatial origins of perceptual alternations are biased toward the location of greatest orientation contrast in the suppressed stimulus. Having shown that orientation contrast is an image feature affecting the spatial origin of perceptual alternations, Experiment 2 aimed at uncovering whether the degree to which the spatial origin is biased towards the location of greatest orientation contrast in the suppressed image is related to the saliency of that orientation contrast. We hypothesized that it is the degree of saliency that is the common denominator of our results from Experiment 1 and the results of Paffen et al. (2008) and Lee et al. (2005; 2007). Note that an increase in orientation contrast does not necessarily result in an increase in saliency. As outlined above, saliency can be defined as the degree to which an item stands out from its surroundings (Yantis, 2005; Altmann, Deubelius & Kourtzi, 2004). Although one oriented item may deviate more from its surround than another, perceptually, they may be equally salient, especially for greater orientation deviances. To assess the degree of saliency at different orientation contrasts, we employed a visual search task where observers search for different target Gabors with orientation deviances ranging from 5 to 90°. In visual search, targets of high saliency will be detected faster compared to targets of low saliency (e.g. Wolfe, Friedman-Hill, Stewart & O'Connell, 1992; Joseph & Optican, 1996). Based on these results, search performance is expected to increase with increasing probe deviance, thereby defining an increase in saliency of the probes. In a separate task, we used the targets from the search task as probes in a binocular rivalry task similar to that of Experiment 1. Again, we measured the origins of perceptual alternations. Using visual search performance as a measure reflecting saliency, we can test whether the spatial bias in the origins of perceptual alternations builds up gradually, increasing as local saliency increases, or whether a certain degree of saliency is sufficient for a fixed amount of spatial bias towards the salient location. If the spatial bias builds up gradually, the amount of spatial bias will increase with increasing saliency. If a certain amount of saliency is sufficient, a fixed amount of spatial bias will occur after a certain degree of visual saliency. The following experiment thus contained two parts: one in which observers searched for a target defined by an orientation contrast of varying magnitude, and one in which observers reported origins of perceptual alternations as in Experiment 1, now using the same images as used in the search task.

Methods

Observers

A total of 8 observers, including two of the authors (ss and cp) and two observers from Experiment 1, took part in the experiment. All had normal or corrected to normal vision and, except the authors, were naïve as to the goals of the experiment. All observers were experienced psychophysical observers and used to performing in experiments dealing with binocular rivalry.

Apparatus

The equipment was identical to that in Experiment 1.

Stimulus and Procedure for the visual search experiment

The search display used for this experiment was similar to the test-image used in Experiment 1 (right image of Figure 4). The display consisted of 169 Gabors aligned on a grid. Parameters of the Gabors were the same as in Experiment 1. In all trials, one of the Gabors, the target, was oriented 0, 5, 10, 20, 45 or 90° clockwise relative to its neighbours. Note that, for the visual search experiment, deviant Gabors are referred to as targets instead of probes since they are part of the observers' task. For the visual search experiment, the 0° deviancy condition refers to *target absent* trials similar to the *probe absent* condition of Experiment 1. As in Experiment 1 (as well as the rivalry experiment outlined below), there were 4 possible target locations; upper left, lower left, upper right or lower right relative to fixation. The distance of the target from the fixation cross was always 2.3°. The smaller distance (compared to Experiment 1) was chosen in order to make the search task not too demanding. The display was presented in green (35.6 cd/m^2, CIE coordinates: x = 0.291, y = 0.608), for reasons related to the binocular rivalry experiment (outlined below). The image was presented simultaneously to the left and right side of the centre of the screen and observers fused the images via a mirror stereoscope to keep the conditions of presentation similar to the rivalry experiment. Half of the trials contained a target. Observers were instructed to indicate as fast and accurately as possible, via key press, whether a deviant Gabor was present or absent. Observers were also instructed to refrain from making eye movements while the search display was present. Each observer completed 400 trials; 200 target-present trials, with 40 trials for each orientation contrast, and 200 trials with no target presented.

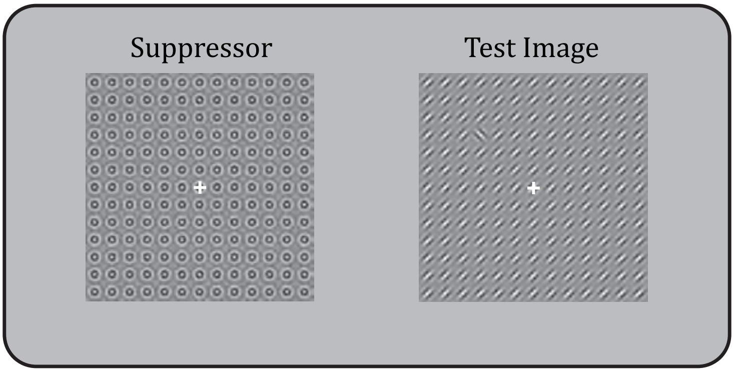


Figure 4:
A schematic representation of the stimulus used in Experiment 2. The suppressor, displayed on the left, consisted of concentric circles. The test-image is displayed on the right (here containing a 90° deviancy probe in the centre of the upper left quadrant). To make the task easier for the observers, the test-image was presented in green and the suppressor in red.

Stimulus and Procedure for the binocular rivalry experiment

The test-images used in the binocular rivalry experiment were identical to those used in the visual search experiment. In this experiment, 20% of the trials contained the *probe absent* condition. For the suppressor we used a 13x13 grid of concentric circles (Figure 4). These concentric circles were filtered with a Gaussian with the same parameters as the Gabors so that the size of circles and Gabors were equal. As in Experiment 1, fusion of the images was aided by presenting a white square around, and a white fixation cross at the centre of the images. The dimensions of these were the same as in Experiment 1. For this experiment the test-image was presented in green (35.6 cd/m^2, CIE coordinates: x = 0.291, y = 0.608) and the suppressor in red (9.3 cd/m^2, CIE coordinates: x = 0.627, y = 0.342). The colours in the images were added in order to make the task easier for the observers. The procedure for presenting the stimulus was the same as in Experiment 1. Observers were instructed to respond as soon as they perceived the colour green anywhere in the display and indicate this with a space-press. The procedure for indicating the spatial origins of perceptual alternations was identical to that of Experiment 1. Each observer completed 432 trials; 72 trials for each orientation contrast and 72 trials with no probe presented.

Results: visual search

In order to assess search performance, we analyzed median reaction times of correct trials of each observer. Overall accuracy of all observers was above 88% (mean = 93%, standard deviation = 4%). However, performance for the 5° target condition was at chance level for several observers, demonstrating the lack of conspicuity of this target. Since the low performance for this condition renders the corresponding reaction times un-interpretable, we opted to remove this condition from further analyses. Removal of this condition lifted overall accuracy to 99%. When no target was present, the average median reaction time across observers for signalling the absence of a target was 2.37 s (sd = 1.55 s; Figure 5). For the 10° deviance target, observers detected the target on average within 0.66 s (sd = 0.12 s). As target-deviance increases, reaction times dropped of to approximately 0.53 s. An ANOVA revealed significant differences among reaction times [$F(3,28) = 4.11$, $p < 0.05$] for different target orientations. Post hoc comparisons show significant decreases in reaction times between the 10 and 20° targets [$t(14) = 2.19$, $p < 0.05$, one-sided]. The reaction times between 20, 45 and 90° deviance targets did not differ, showing a floor effect for search performance. These results suggest that for a target-deviancy of 20° and onwards, increasing target deviancy no longer reduces search times (slope = 0.008 s/deg, $r_{Pearson} = -0.64$, $p = 0.55$), indicating efficient search (Wolfe, 1998). Also, this shows that targets of 20° and onwards do not differ in the degree they stand out from their surrounding, e.g. have similar visual salience. When deviancy becomes smaller than 20° , visual search times first begin to increase (10° target) and followed by a drop in accuracy (5°), indicating the deviant Gabor appears to stand out less from its surround and search of the scene becomes inefficient. Note that, since saliency refers to the degree to which an item stands out from its surroundings, these results validate the manipulation of probe saliency in both Experiments 1 and 2.

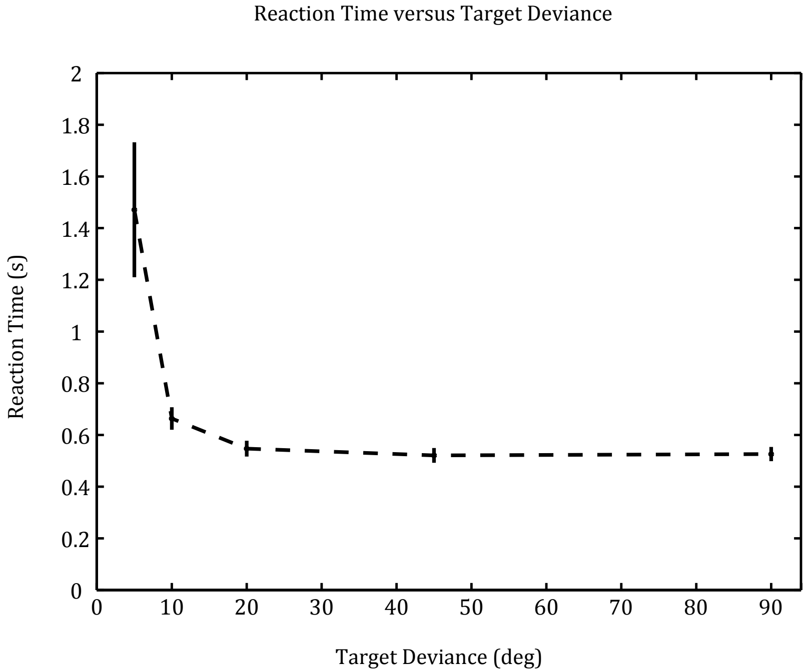


Figure 5:
The average median reaction times for correct target-present trials for the different target deviances. The dashed line represents the average median reaction time for target absent trials. Reaction times decrease with increasing probe deviance. The 5° target data point is not represented in the figure. Due to low performance on this condition, the corresponding data has not been used in the statistical analyses. Error bars represent the standard error. Note that 0° target deviance refers to the target-absent condition.

Probe orientation	Upper Left Quadrant		Upper Right Quadrant		Lower Left Quadrant		Lower Right Quadrant	
0°	1.73 %	22.40%	2.26%	30.90%	1.39%	23.44%	1.39%	16.49%
5°	2.43%	22.40%	1.74%	24.65%	1.56%	22.05%	2.95%	22.22%
10°	5.73%	24.48%	2.60%	22.05%	2.60%	21.18%	1.39%	19.97%
20 °	9.55%	23.78%	3.30%	18.58%	2.08%	20.49%	2.26%	19.97%
45 °	11.11%	20.49%	2.26%	20.49%	2.26%	18.58%	2.08%	22.74%
90 °	11.91%	22.40%	2.60%	19.97%	1.22%	21.35%	1.91%	18.75%

□ Probe area

░ Potential probe area

▓ Non probe area

Table 2:
Table 2 displays the average percentage of responses indicating perceived locations of alternations per image-quadrant per probe angle. The percentages of responses are further subdivided into responses falling within the probe area (for the upper left quadrant) or potential probe area (for the other quadrants) and the regions outside the (potential) probe area. Note that a probe angle of 0° refers to the probe-absent condition. Also note the increase in the percentage of responses with increasing probe deviance for the upper left image quadrant in the probe area.

Results: rivalry

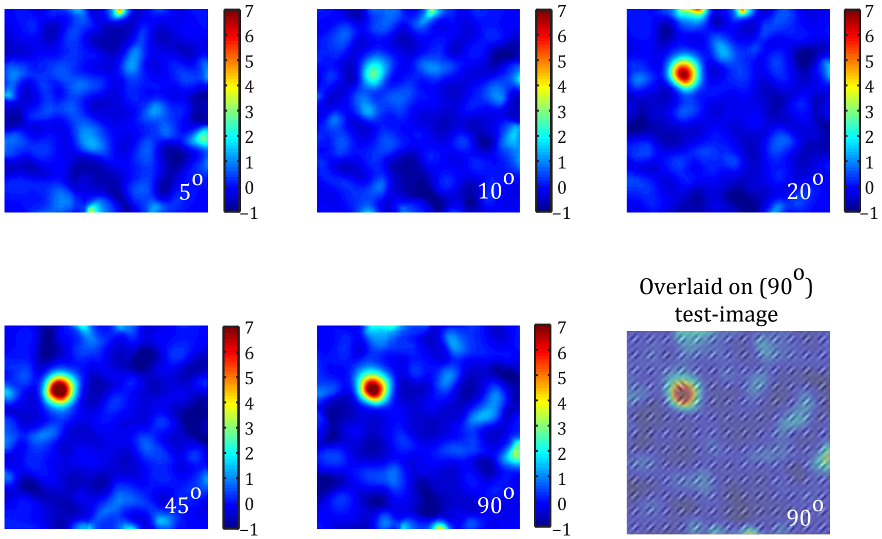
The results were analyzed as described in the results section of Experiment 1, resulting in a total of 6 matrices: 5 for each *probe present* condition (the different rotation-angles of the probe), and one for the *probe absent* condition. These 6 matrices were converted to 5 matrices of Z-scores (Figure 6A; one for each rotation-angle of the probe). These matrices reveal a significant bias in perceived origins of perceptual alternations towards the probe location for all but the 5 and 10° deviance probes (5° deviance, $Z = 0.61$; 10° deviance, $Z = 2.74$; 20° deviance, $Z = 6.83$; 45° deviance, $Z = 8.60$; 90° deviance, $Z = 7.61$), extending and replicating the results of Experiment 1. Comparing across the different deviancies of the probe, responses become increasingly biased towards the probe location as shown by an increase in the peak amplitude on the probe location (Figure 6B).

Similar to Table 1 for Experiment 1, Table 2 presents the average percentages of responses for 8 regions of the results matrix for the different probe angles. The probe-areas are again defined by a 0.8° circular region centred on the probe location in the upper left quadrant or the area where a probe could have been presented for the other 3 quadrants. In the same manner as for Experiment 1, we quantified the bias to potential probe areas by comparing the average percentage of responses to the potential probe areas to the responses to the non-probe areas, corrected for the size of the area, for the absent trials. The results of the probe-absent trials indicate that observer were 3.8 times more likely to indicate a potential probe area compared to an area of similar size within a non-probe area. We also compared the responses to the location of the probe in the present trials to the same size-corrected non-probe areas (see Result section of Experiment 1). When a probe was indeed presented in this area, this bias increased from a ratio 5.5 for the 5° probe, to a ratio of 26.9 for the 90° probe.

The highest Z-scores on probe locations are displayed in Figure 6B. For small probe deviances, peak Z-scores are low (indicating small biases towards the probe locations). However, as probe deviance increases, Z-scores become larger until they plateau at about 20° deviance. Although the spatial bias towards the probe increases with probe deviance, note that spatial bias is more closely related to search performance (Figure 7). While orientation contrast increases monotonically, search performance and spatial bias do not. Both this bias and search performance stay relatively stable once 20° deviance is reached. When visual search for a target is inefficient (right side of Figure 7), using that target as a probe in the rivalry experiment results in low Z-scores (e.g. low spatial bias). Note that, although the combination of rivalry and search performance data for the 5° target/probe is not included in this figure due to low performance in the visual search task, this low performance corresponds nicely to the lack of any spatial bias effects found in the rivalry task. When visual search becomes more efficient (left part of Figure 7), the spatial bias increases. These results show that spatial bias towards areas containing the probe is closely related to search performance. When search efficiency reaches a plateau, so does the spatial bias in the origins of perceptual alternations. Correspondingly, search performance and spatial bias show a linear relation ($r_{\text{Pearson}} = -0.99$, $p < 0.05$). These result show that the amount of bias for reporting a location containing a different orientation in the suppressed image is more closely related to the degree to which the item stands out from its surroundings on a perceptual level (i.e. our search results) than to the amount of orientation contrast.

A)

Spatial Bias per Probe Deviancy



B)

Spatial Bias versus Probe Deviance

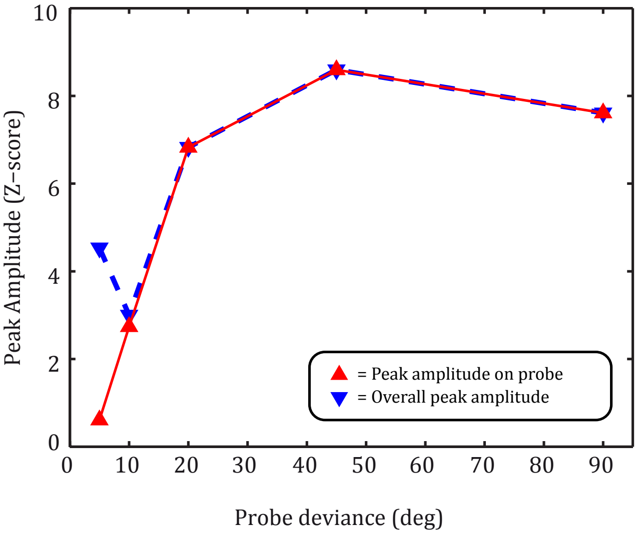


Figure 6:

A summary of the results for the binocular rivalry experiment. Figure 6A depicts the Z-scores, representing reported origins of perceptual alternations, for each probe deviance. Also, an example of the results overlaid on the 90° deviance test-image is displayed. Note that responses become more biased towards the location of the probe (centre upper left quadrant) as deviance of the probe increases. B) Peak of Z-scores for different probe deviances. Red, upward triangles represent the peak amplitude of the spatial distributions (as Z-score) on the probe location and the blue downward triangles represent the overall greatest peak of the spatial distributions. Note that for the probe deviancies of 20° and larger, the greatest peak amplitude corresponds to that of the probe location.

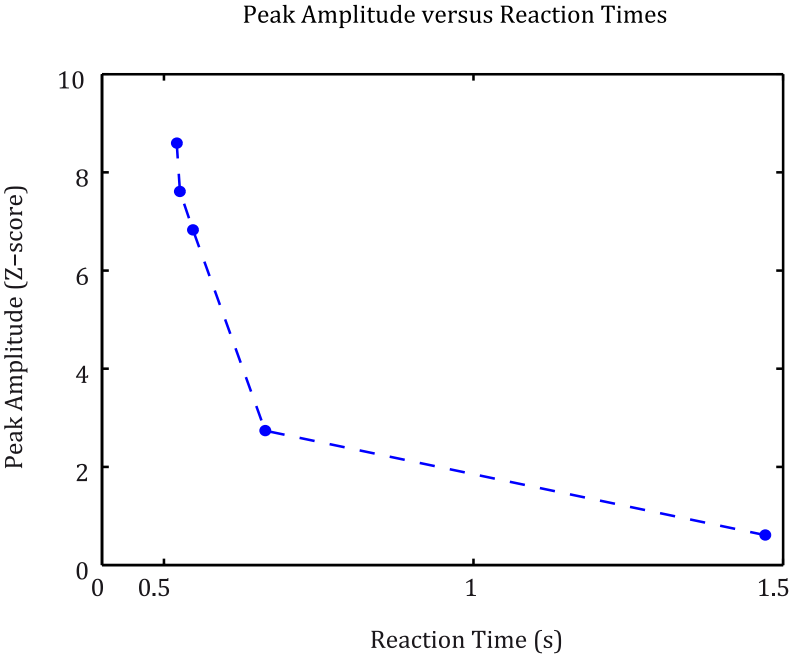


Figure 7:

The highest Z-scores of the different probes corresponding to the probe location plotted against visual search reaction times. Note that for salient targets, where reaction times are small, there is a strong bias for perceptual alternations to start at the probe location. This bias decreases systematically as reactions times increase.

General Discussion

The aim of the current study was to test whether the origins of perceptual alternations during binocular rivalry are biased towards the location of greatest orientation contrast in the suppressed image and, if so, if this bias is related to saliency as inferred from search performance. Our results from Experiment 1 support the first hypothesis: perceptual alternations are affected by intraocular image differences and most frequently originate from the location of greatest orientation contrast in the suppressed image. Note that observers in our study were unaware of any such location of increased orientation contrast before a perceptual alternation occurred. In Experiment 2 we show that when interocular image differences increase, the origins of the perceptual alternations becoming increasingly biased to the location of these differences. Moreover, the results support our second hypothesis by showing a relationship between search efficiency of a probe location in an image (assessed separately by a visual search task) and the degree to which perceptual alternations originated at that location. The use of our visual search task validates the manipulation of saliency in our rivalry tasks by showing that the manipulation of the target orientation affects the degree to which targets stand out from their surroundings. Importantly, the amount of bias for a location containing the orientation contrast was more closely related to efficiency of search, than to amount of orientation contrast (compare Figure 6B and Figure 7). Thus, bias more related to the saliency of the orientation contrast than to the amount of orientation contrast. The relation with saliency suggests that previous manipulations of the origins of perceptual alternations are also based on saliency variations of the suppressed image (Lee et al., 2005; 2007; Paffen et al., 2008).

As put forward in the Introduction, centre-surround interactions at the neural level are a good candidate for an underlying mechanism. In the context of the present study, we suggest that surround suppression and/or surround facilitation alter the relative strength of the Gabors in the suppressed image: the similar orientations are suppressed and/or the orthogonal orientation is facilitated. This hypothesis is supported by the fact that centre-surround interactions have been implicated in contextual modulations of binocular rivalry (Fukuda & Blake, 1992; Paffen, te Pas, Kanai, van der Smagt & Verstraten, 2004; Paffen, van der Smagt, te Pas & Verstraten, 2005; Paffen, Alais & Verstraten, 2005; Sobel & Blake, 2002). Note that such interactions have also been implicated to be responsible for low-level, bottom-up saliency maps (Itti & Koch, 2000).

Implications for theories of binocular rivalry

An influential theory on binocular rivalry states that perceptual alternations are caused by reciprocal inhibitory connections between monocular channels representing the input from each eye (Blake, 1989). An important aspect of this theory is the non-specificity of binocular rivalry suppression: suppression was argued to non-selectively weaken all inputs presented to the suppressed eye (Blake, 1989; Blake & Logothetis, 2002). This idea is based on studies showing that suppression acts on various kinds of probes presented to the suppressed eye (Blake & Fox, 1974; Blake, Westendorf & Overton, 1980; Fox & Check, 1968; Zimba & Blake, 1983; Nguyen, Freeman & Wenderoth, 2001). However, recent evidence suggests that there *can be* specificity in suppression (O'Shea & Crassini, 1981; Alais & Parker, 2006; Apthorp, Wenderoth & Alais, 2009; Stuit, Cass, Paffen & Alais, 2009). We have recently shown that rivalry suppression is dependent on the degree to which probes presented to the suppressed eye match the features driving the interocular competition (Stuit et al, 2009). Our results supply further evidence that suppression is *not* homogeneous across the suppressed image. Importantly, our results show that suppression can vary within an image when the amount of interocular conflict is constant. Previous results on the spatial origins of perceptual alternations (Paffen et al., 2008; Wilson et al., 2001; Lee et al., 2005; 2007) did not allow for dissociation between the relative contributions of inter- versus intra-ocular effects. However, in the current study, although the degree of local interocular conflict was similar at all Gabor locations, the location of greatest saliency in the suppressed image systematically entered dominance first, suggesting that suppression was weakest at that location. This indicates not only interocular image difference (e.g. Stuit et al., 2009) but also intraocular image characteristics can also influence the degree of suppression during binocular rivalry.

Implications for models on visual saliency

A common assumption concerning saliency is that, after systematic extraction on basis of features such as local orientation, it is represented in the visual system in form of a *saliency map*, which topographically codes local conspicuity over the entire visual field (Koch & Ulman, 1985; Itti & Koch, 2000). Previous findings have suggested several candidate brain structures for such a saliency representation, including the pulvinar (Robinson & Peterson, 1992), superior colliculus (Kustov & Robinson, 1996) and the posterior parietal cortex (Gottlieb, Kusunoki, Goldberg, 1998). Recent evidence considers a role of early visual cortical areas in saliency representations (Li, 1999, 2002, 2008). For instance, V1 neurons increase their spiking rate as the saliency of their inputs increase (Li, 1999). Also, during visual search, ocular singletons attract attention automatically, reflecting their saliency (Li, 2008). Note that ocular singletons are defined by eye-of-origin information and that this is largely lost after V1, since neurons with monocular inputs are far more common in V1 as compared to other cortical visual areas (Hubel & Wiesel, 1968; Zeki, 1978). This supports a role for the primary visual cortex in the representation of saliency. Important to the ideas about the neural underpinnings of visual saliency is that the alternations in perception during binocular rivalry have been linked to conflict between monocular inputs to V1 (Blake, 1989; Tong & Engel, 2001). As perceptual alternations in our study started at the location of invisible salient locations presented monocularly, our results support the idea that visual saliency is represented at an unconscious, monocular level of visual processing (Li, 2008).

Chapter 5:

What’s grouping during rivalry?

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Abstract

During binocular rivalry, perception alternates between dissimilar images presented dichoptically. Although perception during rivalry is believed to originate from competition at a local level, different rivalry zones are not independent: rival targets that are spaced apart but have similar features tend to be dominant at the same time. We investigated grouping of spatially separated rival targets presented to the same or to different eyes and presented in the same or in different hemifields. We found eye-of-origin to be the strongest cue for grouping during binocular rivalry. Grouping was additionally affected by orientation: identical orientations were grouped longer than dissimilar orientations, even when presented to different eyes. Our results suggest that eye-based and orientation-based grouping is independent and additive in nature. Grouping effects were further modulated by the distribution of the targets across the visual field. That is, grouping within the same hemifield can be stronger or weaker than between hemifields, depending on the eye-of-origin of the grouped targets. We also quantified the contribution of the previous cues to grouping of two images during binocular rivalry. These quantifications can be successfully used to predict the dominance durations of different studies. Incorporating the relative contribution of different cues to grouping, and the dependency on hemifield, into future models of binocular rivalry, will prove useful in our understanding of the functional and anatomical basis of the phenomenon of binocular rivalry.

Introduction

During binocular rivalry, dissimilar images presented dichoptically compete for awareness. As a result, perception varies over time (e.g. Wheatstone, 1838). When large images are engaged in rivalry, perception often consists of a patchwork combination of the competing images. That is, different locations have different perceptual outcomes (e.g. Meenes, 1930), implying that the dominant percept contains parts of both the left and the right eye's image. This patchwork or piecemeal rivalry does not occur when the images are rather small (estimated at 5-7 min of visual angle in the fovea; Blake, O'Shea and Mueller, 1992). These observations reveal an important characteristic of rivalry, namely that it is a local phenomenon. Investigations into this local nature of rivalry revealed that the size of local rivalry zones scales with eccentricity and may correspond to the size of the receptive fields in the hypercolumns of early visual cortex (Blake, et al., 1992).

Although perception during rivalry seems to be determined at a local level, different rivalry zones are not necessarily independent: similar (parts of) images tend to be dominant in perception together. That is, adjacent rivalry zones tend to produce the same dominant percept when neighbouring zones share similar features like motion or colour, even when this information is distributed across the two eyes (e.g. Whittle, Bloor and Pocock, 1968; Kovács, Papathomas, Yang and Fehér, 1997; Alais and Blake 1998). For instance, Kovács and her colleagues created rival targets consisting of patchwork combinations of two complex images. Each eye received only part of the originals when they were presented dichoptically. The perceptual outcome during rivalry often consisted of a coherent reconstruction of the original images (Kovács, et al., 1997; also see Diaz-Caneja, 1928, translated by Alais, O'Shea, Mesana-Alais and Wilson, 2000). Interestingly, this reconstruction required simultaneous dominance of rivalry zones across both eyes; an effect known as interocular grouping. Similar effects have been found for grouping of spatially separated items (e.g. Whittle et al., 1968). Alais and Blake (1999) demonstrated that similar rival targets that were separated spatially also tend to be dominant at the same time, an effect referred to as *joint predominance*. They showed that Gestalt grouping-cues were effective in increasing the joint predominance of rival targets: Joint predominance was larger for parallel and collinear grating-pairs compared to that of orthogonal gratings. Also, correlated contrast modulations of the gratings increased joint predominance in comparison to uncorrelated contrast modulations.

These results show how the dominant percept originating from a local rivalry zone is affected by the dominant percept of neighbouring rivalry zones. Furthermore, since the effect of joint predominance decreased with angular separation between the rivalling targets, Alais and Blake argued that interactions between lateral connections of the cortical hypercolumns were responsible for their effect.

Together, the above results suggest that the perceptual outcome of two rivalling images is primarily determined at a local level, but that grouping[1*] cues (like good continuation) affect the local competition: when two adjacent regions contain similar image content, the images tend to be dominant in perception at the same time, even when the image content is distributed across the two eyes.

The current study has two aims. First, we want to assess the strength of grouping when rival images are presented to the same versus different eyes and presented in the same versus different hemifields. This allows us to link grouping strength to known aspects of functional visual pathways. As Alais and Blake (1999) suggested, grouping during binocular rivalry might be related to connections at the level of the primary visual cortex. Estimating the grouping strength between targets that have very different cortical representation loci (i.e. represented in different ocular dominance columns and different hemispheres) will provide more insight in the effective connectivity that drives grouping during rivalry.

Our second aim is to elucidate the relative contributions of stimulus-based versus eye-based rivalry during simultaneous dominance of spatially separated targets. Interocular grouping and stimulus-based rivalry both emphasize competition based on image-content over competition based on eye-of-origin of the images. Theories suggesting that rivalry competition is resolved at ‘later stages’ of visual processing rely on examples of stimulus-based rivalry, such as Flicker-and-Swap-rivalry (Logothetis, Leopold, and Sheinberg, 1996). These ‘later stages’ are meant as relatively later to those put forward in the many studies emphasizing the low-level nature of binocular rivalry. For example, Blake (1989) argued that monocular neurons are crucial for the initiated of binocular

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1* In this study, grouping refers to the simultaneous dominance of two rival targets. When referring to grouping effects found in other studies, we will use the terminology of the original authors (i.e. interocular grouping or joint predominance).

rivalry. The necessity of monocular neurons thus limits rivalry competition to be initiated early in the visual processing hierarchy. Both early and late theories have gained support from psychophysical as well as imaging studies (Polonsky et al., 2000; Tong and Engel, 2001; Silver and Logothetis, 2007). In recent years, these different views have started to converge to the idea that rivalry is resolved at multiple stages along the visual hierarchy (Blake and Logothetis, 2002; Silver and Logothetis, 2007; Freeman, 2005; Lee, 2004; Nguyen, Freeman, and Alais, 2003; Wilson, 2003). In accordance with this idea, stimulus-based rivalry has been suggested to have a synergetic effect on eye-based dominance periods (Kovács et al., 1997; Lee and Blake, 2004). Determining perceptual dominance durations for different percepts of separate rival targets, presented either to the same or to different eyes, allows us to investigate this in more detail.

Since we know that collinear and parallel gratings tend to group during rivalry, we presented such targets under various spatial arrangements. In our experiments, we presented identical, spatially separated, rival targets (1) to the same or different eyes, and (2) in the same or different hemifields. Estimating the relative strength of grouping two images under these different arrangements allowed us to dissociate low-level, eye-based contributions to perceptual grouping from high-level, pattern-based contributions. Next, we implemented their relative contributions in a simple descriptive model based on the known functional anatomy of primary visual cortex.

Methods

Observers

A total of 12 observers, including one of the authors (SS) participated in the study. 8 observers participated in the main experiment and 7, including 4 observers from the main experiment, participated in a separate version of the experiment (see below). All had normal or corrected to normal vision and all but SS were naïve as to the purpose of the study. All observers were experienced psychophysical observers and passed a test for stereo vision (TNO test for stereoscopic vision). All observers gave informed consent before participating.

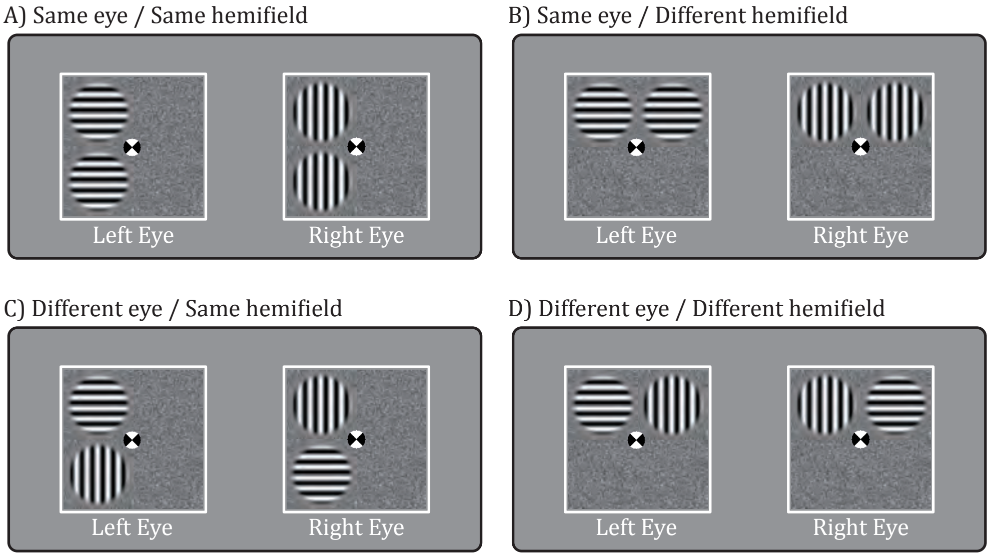


Figure 1: Presentation conditions.
The four different stimulus arrangements used. The rival targets were presented such that identical targets were presented (A) in the same hemifield for the same eye; (B) in different hemifields for the same eye; (C) in the same hemifield but for different eyes; or (D) in different hemifields and for different eyes. All presentation conditions were counterbalanced for eye and hemifield. Note that all rival targets have the same distance to each other as well as to the fixation point.

Apparatus

Stimuli were created on an Apple Mac Pro computer running system OS-X and Matlab 7.4 with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). The stimuli were presented on a linearized LaCie III 22" at 75 Hz. Observers viewed the stimuli through a mirror stereoscope. The length of the optical path was 57 cm.

Stimuli

The rival stimuli were two pairs of half-images each consisting of two sine-wave gratings. To initiate rivalry, each interocular pair had orthogonal orientations (Figure 1). The gratings were presented at maximum contrast (98% Michelson Contrast, space-average luminance: 24.83 cd/m^2). The rivalling gratings (spatial frequency 4.1 cpd, diameter 1.65°) appeared in circular apertures of which the edges were softened by a cosine ramp of 0.2° of visual angle, and were presented on a random pixel noise background of 98% (Michelson) contrast (mean luminance 24.83 cd/m^2) that was identical in both eyes. The half-images were presented within a white square. We used four basic grating arrangements in our experiment (Figure 1): same orientations in the same hemifield – for the same eye: (A), same orientations in different hemifields – for the same eye: (B), same orientations in the same hemifield – for different eyes: (C), and same orientations in different hemifields – for different eyes: (D). All presentation conditions were counterbalanced for eye and hemifield. This resulted in each orientation being presented to each eye and in each hemifield equally often. The distance from the fixation point to the centre of the target was identical for all targets in all conditions (2.1° of visual angle). Two versions of the gratings pairs were used. In the main experiment we used horizontal and vertical grating pairs. Such gratings have been shown to result in perceptual grouping by Alais and Blake (1999). In a second version of the experiment we used oblique gratings, two of which were tilted 45 degrees clockwise and two that were tilted 45 degrees counter clockwise from vertical. Comparing the results of two versions of the experiment can provide insight into whether having identical image-content is sufficient for grouping during rivalry.

Procedure

Observers performed the experiment in a darkened room with their heads stabilized by a chin rest. Before the onset of each trial, observers were presented with two identical pixel noise half-images surrounded by white frames. At the centre of each half-image was a fixation point. When ready, an observer initiated a trial by pressing the space bar. Next, two pairs of orthogonal gratings were presented in one of four possible spatial arrangements. Observers performed a 2AFC perceptual tracking task where they indicated via a key press, whether they perceived two identically oriented gratings (right arrow key), or two orthogonal gratings (left arrow key). In case of a mixed percept, observers were still required to make a forced-choice. Note that the use of small gratings kept the occurrence of mixed percepts at a minimum (Blake, O'Shea and Mueller, 1992). Each trial lasted 30s. After each trial, the rivalling targets were removed from the screen. Observers were instructed to fixate on the fixation point throughout the experiment.

Results

For our analyses we used two measures for grouping during rivalry: 1) Fractions of simultaneous dominance (i.e. the fraction of time images had the same or different orientations) and 2) epoch durations (i.e. the time an observer had one of these percepts). To get a first impression of the biases for grouping during rivalry we first discuss the fractions for simultaneous dominance of targets with identical cardinal orientations, followed by the underlying dominance epochs that resulted in these fractions for dominance. Subsequently, we will address the data for grouping oblique orientations. Where applicable, the p-values were corrected for multiple comparisons.

Our first analyses concerned the fractions of simultaneous dominance for cardinal orientations presented in the *same* or *different* hemifields and to the *same* or *different* eyes. The fractions were calculated using the time observers actually responded. This means that the duration of each trial that observers did not respond was subtracted from the 30s trial-duration before calculating the fractions. The fractions of simultaneous dominance were interpreted as an indication of bias towards or away from grouping identical orientations. A fraction of 0.5 means that identical orientations were as often perceived as dissimilar orientations and perception was thus *unbiased* with respect to grouping.

We compared the fraction of simultaneous dominance of identical orientations across our four presentation conditions; identical orientations presented to (1) the same eye and within the same hemifield, to (2) the same eye but within different hemifields, to (3) different eyes but within the same hemifield, or to (4) different eyes and in different hemifields (Figure 2). A two (eye) by two (hemifield) repeated measures ANOVA revealed a main effect of eye ($F(1,7) = 45.45$, $p < .001$, $\eta_p^2 = .867$), but not of hemifield ($F(1,7) = 0.66$, $p = .689$, $\eta_p^2 = .086$). However, an interaction between the two was apparent as well ($F(1,7) = 11.19$, $p = .024$, $\eta_p^2 = .612$). To test the nature of the interaction we compared the effect of hemifield in the *same-eye* conditions to the *different*-eye conditions. Hemifield-effects were defined as the difference between the fraction of simultaneous dominance of identical orientations when presented in the *same versus different* hemifield(s) (i.e. the difference between the white and the dark grey bars in the *Same Orientation* panels of Figure 2). The result showed that the hemifield-effect differed depending on the (same- and different-) eye condition (paired sample t-test: $t(7) = 3.34$, $p = .0245$, Cohen's $d = 1.18$). The interaction between eye and hemifield reflects the reversal of this hemifield-effect: When identical orientations were presented to the same eye, presenting those orientations in the same hemifield *increased* grouping compared to the presentation in different hemifields. However, when identical orientations were split between the eyes, presentation in the same hemifield *decreased* the fraction of simultaneous dominance.

Each fraction of simultaneous dominance of identical orientations was subsequently tested for a bias towards orientation-based grouping using paired samples t-tests. The results show that when identical orientations were presented to the same eye, there was a bias towards grouping for both the *same* and *different* hemifield conditions ($t(7) = 16.83$, $p < .001$, Cohen's $d = 5.95$; $t(7) = 6.47$, $p = .001$, Cohen's $d = 2.29$ respectively). However, when the identical orientations were presented to different eyes, there was no bias towards grouping based on orientation (same hemifield, biased *away* from orientation-based grouping: $t(7) = -3.35$, $p = .048$, Cohen's $d = -1.18$; different hemifields, unbiased: $t(7) = -0.60$, $p = .965$, Cohen's $d = -0.21$). These results show that there is only a bias towards grouping identical orientations when they are presented to the same eye.

The analysis of the fractions of simultaneous dominance suggests that grouping during rivalry primarily occurs between targets presented to the same eye. However, identical fractions can result from very different distributions of dominance epochs. To get a more detailed picture of the effect of grouping on perceptual dominance, we compared the dominance durations for each combination of grouped targets (identical or different orientations).

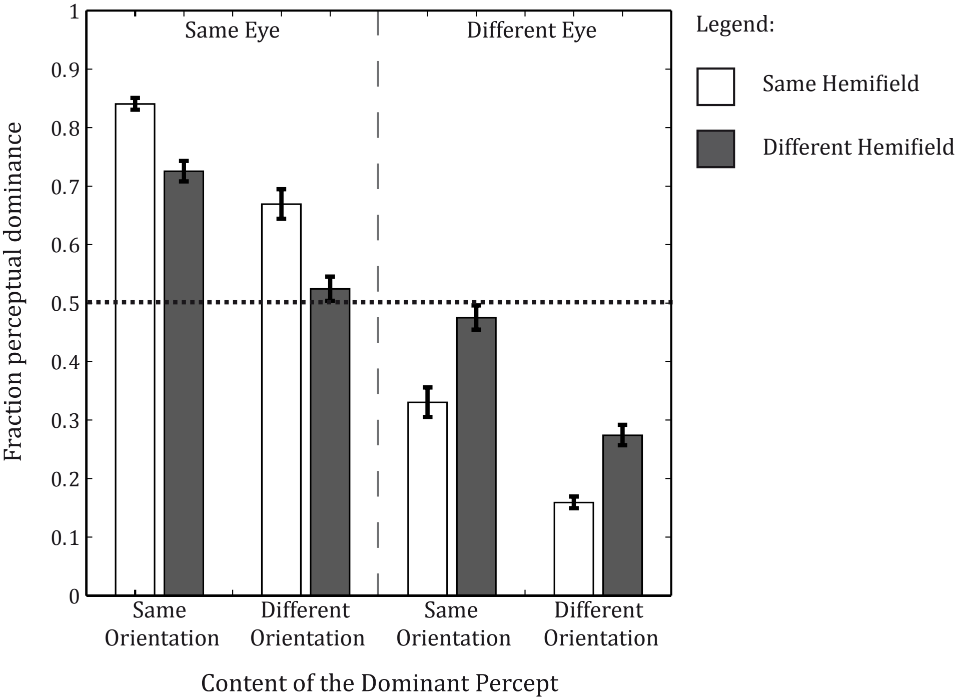


Figure 2: Group means of the dominance fractions
The average fraction of simultaneous dominance across observers for all possible grouped percepts. Error bars represent standard errors of the mean (s.e.m.). Fractions are plotted for each condition. Each bar represents the fraction of dominance for two targets. The dotted line represents unbiased dominance. The results show that when identical rival targets are presented to the same eye, there is a bias towards orientation-based grouping. This is not the case when identical targets are split between the eyes. The bias towards grouping is further increased when identical targets are presented within the same hemifield as well as to the same eye. However, when identical targets are presented to different eyes, the bias is decreased (a bias away from grouping) for presentation in the same compared to different hemifields. These results suggest a strong preference for visual information presented to one eye to be simultaneously dominant.

To calculate the dominance durations we used the median duration (per condition per observer) to correct for the known skewed distribution of dominance epochs (Levelt, 1967). In addition, large individual differences in dominance durations are known to be common as well (e.g. Aafjes, Hueting and Visser, 1966). To correct for the latter, all durations were normalized to each observers' average median dominance duration across all trials, percepts (simultaneous dominance of the same of different oriented gratings) and conditions.

Throughout the experiment, simultaneous dominance of two targets can reflect grouping based on multiple cues: eye-of-origin, hemifield and orientation (Figure 3). The comparison of the average duration of each of these perceptual outcomes can be used to estimate the strength of each grouping cue. Epoch durations for each perceptual outcome were compared using a two (eye) by two (orientation) by two (hemifield) repeated measures ANOVA. We found a main effect for eye (F(1,7) = 61.54, $p < .001$, $\eta_p^2 = 0.898$) as well as for orientation (F(1,7) = 46.14, $p < .001$, $\eta_p^2 = .868$), but not for hemifield (F(1,7) = 1.46, $p = 0.461$, $\eta_p^2 = .172$). As was true for the analysis of the fraction simultaneous dominance of identical targets, we found an interaction between eye and hemifield (F(1,7) = 11.35, $p = .024$, $\eta_p^2 = .619$). This interaction reflects the difference in the hemifield-effect when the same orientations were presented to the same eye versus when they were presented to different eyes (paired sample t-test: $t(7) = 3.37$, $p = .024$, Cohen's $d = 1.19$). No interaction between orientation and hemifield (F(1,7) = 0.07, $p = .960$, $\eta_p^2 = .010$), orientation and eye-of-origin (F(1,7) = 2.30, $p = .316$, $\eta_p^2 = .248$) or three-way interaction was found (F(1,7) = 0.76, $p = .567$, $\eta_p^2 = .097$).

Recent evidence suggests eye-based and image-based influences on binocular rivalry vary over time (Bartels and Logothetis, 2010). Their results suggest epoch duration may become shorter as rivalry continues. Moreover, the first second of rivalry competition has been argued to be fundamentally different from the remaining rivalry period (Carter and Cavanagh, 2007). Using relatively short epoch durations, the first few seconds of each rivalry period may be overrepresented in our data. However, we found no effect of time on the different contributions to grouping in our paradigm statistically nor did we find any apparent trend to the influence of time on these contributions. The only hint to in temporal effects was a slight increase in dominance epochs near the end of the rivalry periods compared to the beginning of the trials.

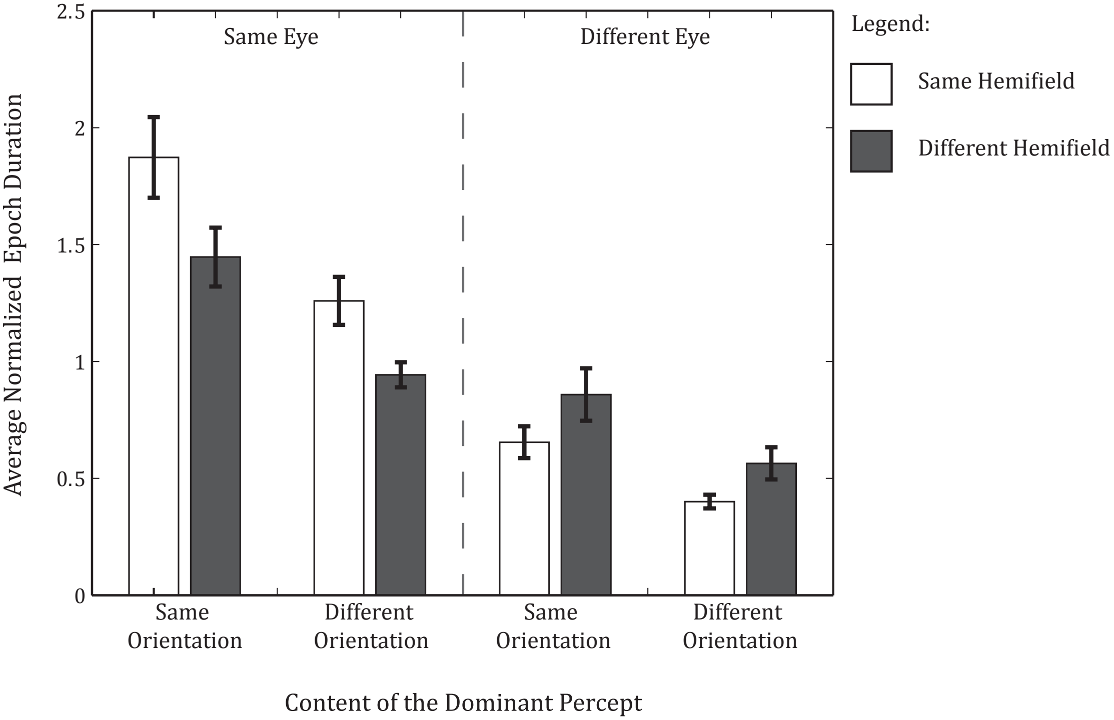


Figure 3: Average epoch duration
Average normalized median durations of each particular perceptual outcome are represented for each condition. All durations are normalized to each observer's median epoch duration across all trials, percepts and conditions. Error bars are s.e.m. Each bar represents the dominance duration that two targets were dominant at the same time. The durations of grouping two targets are separated by the targets' eye-of-origin, the hemifield in which they were presented and their orientation.

The analysis of the fractions of simultaneous dominance suggested grouping is primarily eye-based; there was no bias towards grouping identical orientations presented to different eyes. However, the analysis of the epoch durations *did* show an effect of orientation on grouping: identical orientations are grouped for longer durations than dissimilar orientations. Importantly, this effect was *not* dependent on the eye-of-origin of the grouped targets (e.g. no interaction). This suggests a grouping effect of orientation irrespective of whether the images are presented to the same eye or not. The differential effects of grouping based on eye-of-origin and orientation cannot be fully disentangled by comparisons of the fractions of dominance. However, the analyses of epoch durations appear to be a much more sensitive measure to investigate the different grouping cues. This difference between the fraction and the epoch results is likely to stem from a difference in the underlying distributions of dominance durations; distributions for within-eye grouping were much broader than for between-eye grouping. These characteristics of the underlying distributions are lost in the comparison of the fractions of grouping during dominance. The median durations, however, are less affected by these differences in the underlying distributions.

The next step in our analysis is to quantify the respective contributions of the eye-of-origin and orientation cues for grouping (Figure 4A). The hemifield condition was ignored since the repeated measures ANOVA showed no main effect for hemifield on grouping targets during rivalry. Therefore, simultaneous dominance of two targets can be based on a single cue for grouping (a shared eye-of-origin *or* a shared orientation), on two grouping cues (a shared eye-of-origin *and* a shared orientation), or no grouping cues at all (simultaneous dominance of different orientations targets presented to different eyes). We tested whether the number of grouping cues affected the average median duration of a particular percept. Using paired sample t-tests, we found that the duration of simultaneous dominance based on a single grouping cue is longer than when there are no grouping cues at all (orientation cue: $t(7) = 4.21$, $p = .020$, Cohen's $d = 1.49$; eye-of-origin cue: $t(7) = 10.49$, $p < .001$, Cohen's $d = 3.71$). Also, eye-of-origin provides a stronger grouping cue than orientation ($t(7) = 4.39$, Cohen's $p = .016$, $d = 1.55$). Finally, when both cues are present, the duration of simultaneous dominance is longer than for any single cue alone (compared to orientation: $t(7) = 4.98$, $p = .008$, Cohen's $d = 1.76$; compared to eye-of-origin: $t(7) = 3.89$, $p = .030$, Cohen's $d = 1.37$). These results show the effectiveness of both grouping cues on the duration of particular percept as well as the relative strength of each cue.

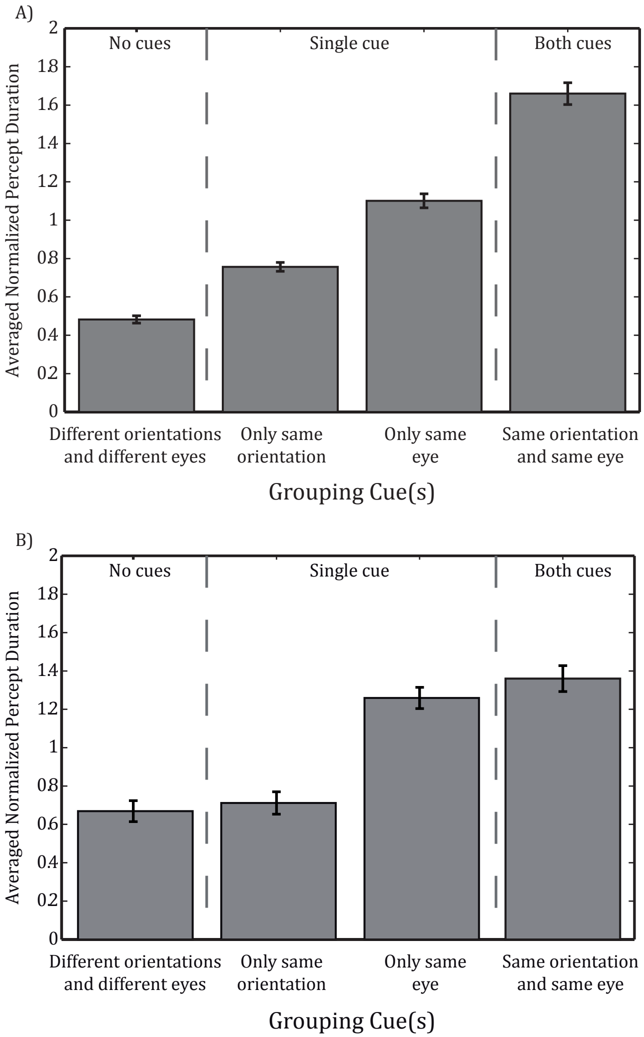


Figure 4: Percept durations per grouping cue

The average median duration of each particular perceptual outcome, represented for each grouping cue. All durations are normalized to each observer's average median epoch duration of all trials, percepts and conditions. Error bars represent s.e.m. The data are arranged based on the number of grouping cues associated with each perceptual outcome. The results are plotted as a hierarchy to illustrate the relative potency of certain grouping cues over others. Figure 4A displays the results for our main experiment using cardinal orientations. Figure 4B displays the results for grouping when oblique orientations are used.

Our final analysis is concerned with the observation that synergistic interactions among neighbouring rivalry zones reinforce perception of coherent patterns during rivalry (Lee and Blake, 2004; Kovács et al., 1997; Blake, 2001). Our results for grouping cardinal orientations confirm this by showing that different cues can combine to have a synergistic effect on the duration of grouping during rivalry. To test the nature of this synergistic effect, we first took the duration of simultaneous dominance of a horizontal and a vertical oriented target presented to different eyes (the left most bar in figure 4A) as the baseline duration for grouping. Next, we subtracted this baseline from the durations of simultaneous dominance based on either one or more grouping cues. These difference scores show the additional contribution to the duration of grouping associated with each cue (Figure 5A). A paired sample t-test showed that the sum of the added durations of simultaneous dominance based on image-content and eye-of-origin is not significantly different from the duration of simultaneous dominance when both these cues are present ($t(7) = 1.52$, $p = .173$, Cohen's $d = 0.54$). This finding concurs with the lack of an interaction between the eye-of-origin and the orientation of the rival targets (see above). In sum, this suggests that the cue effects are independent, and act additively on dominance durations.

The effectiveness of the orientation cue for grouping described above is applicable to cardinal orientations. The same analysis on the data for the experiment using oblique orientations also shows an eye-of-origin effect on grouping rivalling targets ($t(6) = 3.09$, $p = 0.04$, Cohen's $d = 1.17$; Figure 4B & 5B). Note that the effect is similar in magnitude compared to the experiment using cardinal orientations. However, for oblique orientations, we found no effect of the orientation cue to grouping ($t(6) = 0.71$, $p = .757$, Cohen's $d = 0.27$). In addition, analyses of the fractions of dominance when the rivalling grating pairs were oblique (as is represented for cardinal orientations in figure 2) only showed a significant effect of eye-of-origin ($F(1,6) = 13.69$, $p < .01$, $\eta_p^2 = .695$) and of the interaction between eye-of-origin and hemifield ($F(1,6) = 10.58$, $p = .017$, $\eta_p^2 = .638$), but no effect of orientation ($F(1,6) = 1.46$, $p = .272$, $\eta_p^2 = .196$). These results show that cardinal orientations are more readily grouped than oblique orientations during rivalry dominance. Furthermore, the lack of grouping identical oblique orientations suggests that having identical image-content is not sufficient for grouping during rivalry dominance.

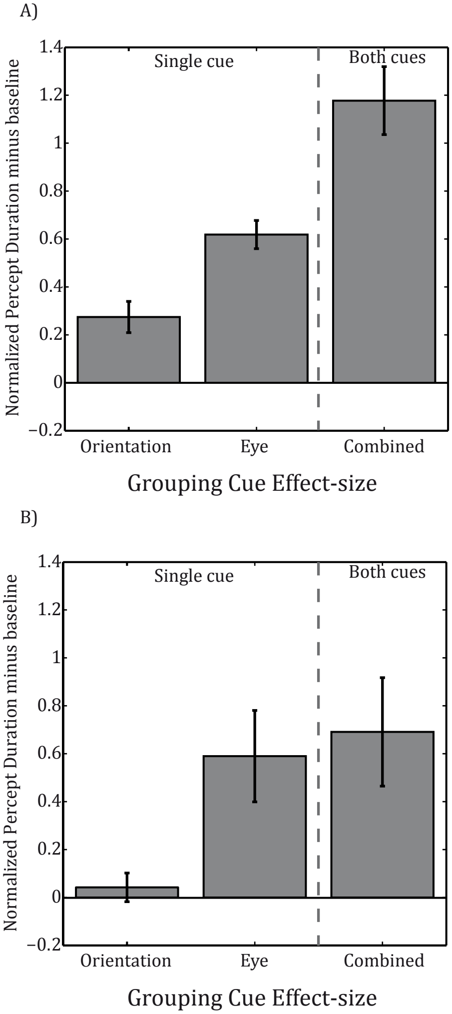


Figure 5: Effect sizes of the different grouping cues
The data from Figure 4, displayed as difference scores by subtracting the baseline dominance duration: the duration of dominance when no grouping cues are present. The difference-scores represent the added percept duration and are represented as a function of cue effect. Note that the sum of both single cues does not differ from the dominance duration when both cues are simultaneously present. We suggest the cue effects are independent and have additive effects on dominance durations. Figure 5A show the data for cardinal orientations. Figure 5B shows the data for oblique orientations.

General Discussion

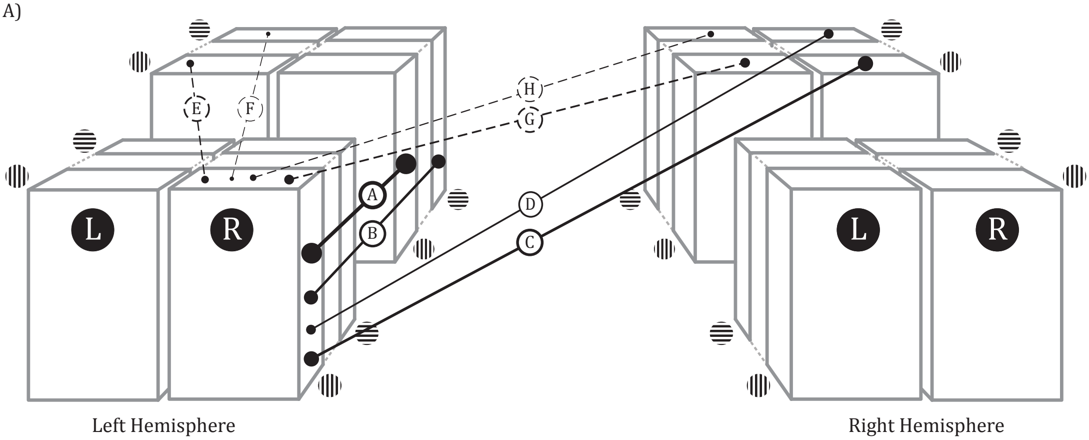
We investigated perceptual grouping of two spatially separated rival targets under a variety of spatial arrangements. Identical rival targets were presented to the same or to different eyes, and within the same or in different hemifields. For cardinal orientations, we found a bias towards grouping when identical orientations were presented to the same eye, but no such bias was evident when identical orientations were presented to different eyes. Moreover, for oblique orientations, grouping during dominance was only affected by eye-of-origin. These results show that eye-of-origin is an important factor for grouping similar orientations during binocular rivalry. The distribution of the targets across the visual field also affected grouping with respect to eye-of-origin. Grouping occurred more often for images presented to the same eye when the images were in the same hemifield. The opposite was true for images that were split between the eyes. That is, images in the same hemifield were grouped *less* often. The modulation of grouping effects by the distribution of the targets across the visual field appears independent of orientation.

The overall occurrence of simultaneous dominance of two targets during rivalry was not biased towards grouping identical orientations across the eyes. However, for cardinal orientations, the *duration* of grouping was affected by orientation irrespective of whether the images were presented to the same eye or not. Our results suggest that eye-of-origin and orientation provided independent cues for grouping during rivalry, with eye-of-origin being the superior cue. It has before been argued that synergistic interactions among neighbouring rivalry zones reinforce the perception of coherent patterns during rivalry (Lee and Blake, 2004; Kovács et al., 1997; Blake, 2001). We present quantitative evidence for a synergy between grouping based on image-content, and eye-of-origin. More specifically, our results show that this synergetic effect is additive in nature. However, we only found an effect of image-content for rivalling grating pairs with cardinal orientations; no such effect was found for oblique orientations. The difference between these results likely stems from the lack of co-linearity when rivalry is between oblique grating pairs. Both psychophysical and physiological studies have shown that facilitation of a flanking line on a target is largest when the lines are collinear (Kapadia, Ito, Gilbert and Westheimer, 1995). However, non-collinear parallel orientations have also been shown to group during rivalry dominance (Alais and Blake, 1999). Since the identically oriented oblique gratings are not collinear but nevertheless parallel, on would expect the grouping effects for the oblique gratings to possibly be smaller, but still present. In the present study, however, no such orientation-based grouping was found for oblique orientations. Therefore, our results suggest that the grouping effects for the oblique gratings, if present at all, are very small. We currently do not have an explanation why we found no orientation-based grouping for oblique grating pairs. One possibility is that parallelism is not a strong cue for grouping when the rival targets are not aligned on an axis orthogonal to their orientation.

The data from this study can be used to calculate the relative contributions for all cues affecting grouping during rivalry: eye-of-origin, orientation and hemifield. These relative contributions of each are taken directly from the normalized epoch durations as reported in Figure 3: the average normalized median durations of simultaneous dominance of two rival targets. The contributions are implemented as weights in Figure 6: a schematic representation of the cortical hypercolumns in early visual cortex. The cartoon is made for descriptive purposes only and we refrain from making strong statements about the anatomical connections underlying the (grouping) weights. A first thing to notice is that grouping is strongest for items presented to the same eye (Figure 6, connections A-D). Whether the items are identical or not, and whether they are processed in the same hemisphere or not, does not affect the generality of the effect. Also, eye-based grouping of two targets is stronger when they are presented in the same hemifield (Figure 6, connection A versus C and connection B versus D). This fits well with the decrease in joint predominance with increasing lateral separation as reported by Alais and Blake (1999), and with the decrease in connection strength as a function of increasing cortical distance (Das and Gilbert, 1995; Bosking, Zhang, Schofield and Fitzpatrick, 1997). However, grouping of targets between the eyes is stronger when they are presented in different hemifields (as compared to presentation in the same hemifield; Figure 6, connections G & H versus connections E & F).

At first sight, this result is counterintuitive, since connections between hemispheres are longer than connections within a hemisphere. We speculate that this result indicates that connections between different eyes are more inhibitory (leading to less grouping) within a hemisphere, compared to between hemispheres. In conclusion, we can draw a hierarchy of different visual structures involved in grouping: grouping of both similar and different orientations is (1) strongest across hypercolumns receiving input from a single eye and hemifield, (2) weaker across hypercolumns from a single eye between

A)



B)

Connection	A	B	C	D	E	F	G	H
Weight	1.87	1.26	1.45	0.94	0.65	0.40	0.86	0.56

Figure 6: Schematic representation of the connections and their weights involved in grouping during rivalry. A) Schematic representation of connections subserving simultaneous dominance. The L stands for the Left eye and the R for the Right eye. The left part of the figure represents the hypercolums in the left hemisphere and the right part the right hemisphere. Each hemisphere has two hypercolumn representations corresponding to different locations in the visual field. Solid lines indicate connections between ocular dominance columns representing the same eye (and different retinal locations). Dashed lines represent connections between ocular dominance columns representing different eyes (and different retinal locations). The thickness of each line is adjusted to the weight of the connection. B) Relative weights of each connection in A. The weight for each line is a direct representation of the data presented in Figure 3.

hemifields, (3) weaker across hypercolumns from different eyes and hemifields, and (4) weakest across hypercolumns from a single eye between hemifields.

Although the above model is first and foremost descriptive for our results, we can use these weights for grouping to try and make quantitative predictions. For example, in their experiment 1, Alais and Blake (1999) measured joint predominance for pairs of collinear, parallel and orthogonal gratings that rivalled with noise patches. The grating-pairs were presented to the same eye but in different hemifields. As such, the results of their parallel and collinear conditions are comparable to our results for perceiving identical orientations presented to the same eye and in different hemifields (i.e. connection C in figure 6). The results for their orthogonal condition are comparable to our results for perceiving different orientations presented to the same eye and in different hemifields (i.e. connection D in figure 6). Our results would then suggest the strength of the links between the collinear and the parallel grating pairs to correspond to the weight of 1.45 and the orthogonal pair to correspond to the weight of 0.94. Based on these weights we would expect the grouping effect for the collinear and parallel gratings to be 1.54 times larger than that for the orthogonal pair. From Alais and Blake's Figure 1B, we see that the fraction of grouping for the orthogonal pair is about 0.31. The fractions for grouping the parallel and collinear grating pairs are about 0.53 and 0.42 respectively. The average fraction of these two conditions (0.475) is thus 1.53 times larger than for the orthogonal condition, almost exactly the same ratio as that follows from our results. Interestingly, the images suppressed during simultaneous dominance of the different grating pairs differed substantially between their study and ours. While we used a second grating pair, Alais and Blake used noise patches to rival with their gratings. Since their results are quantitatively similar to ours, the content of the suppressed images does not appear to affect the relative strength of grouping during dominance. This suggests another interesting feature of grouping during rivalry: the strength of grouping is based on the currently dominant images, not the suppressed ones. Note that the difference between grouping for parallel and for collinear gratings shown by Alais and Blake (1999) suggests that the collinear grating pairs may have had the greatest influence on our grouping results. Since we did not have observers dissociated between the orientations in the dominant percept we cannot test this directly. However, with collinear being a stronger grouping cue than parallel only, this is very likely the case.

Our results also make predictions about the spread of travelling waves typically seen during rivalry alternations (Wilson, Blake and Lee, 2001). From our results we would expect a difference between waves travelling within one hemifield as compared to the across hemifields. Since our data suggests the linking of neighbouring rivalry zones to be stronger within the same hemifield (assuming eye-based dominance of an image) we expect travelling waves to spread faster within hemifields (e.g. vertical spreading) compared to across hemifields (e.g. horizontal spreading). To our knowledge, this has not yet been tested, although the data may already be available (e.g. Blake, Lee and Heeger, 2005). This is not unexpected since models of binocular rivalry do not typically involve any consideration as to which hemifield or -fields the image(s) is presented in (for instance: Blake, 1989; Wilson, 2003; Ashwin and Lavric, 2010). Our results show that incorporation of the hemifield-effect may be critical in predicting dominance durations during binocular rivalry.

To summarize, we investigated grouping of spatially separated rival targets presented to the same or to different eyes and presented in the same or to different hemifields. We found that:

- Eye-of-origin is the strongest cue for grouping during binocular rivalry.
- Identical cardinal orientations are grouped in dominance for longer periods than dissimilar orientations.
- Identical image-content alone is not sufficient for grouping during dominance.
- Eye-based and orientation-based grouping are independent effects and additive in nature.
- Grouping within and between hemifields will increase or decrease depending on the presence of the eye-of-origin grouping cue.

The different contributions to perceptual grouping can be easily quantified and used to make predictions on dominance durations in other studies. Although beyond the scope of the present paper, incorporating these weights, including the dependency on hemifield, into future models of binocular rivalry, may prove useful in our understanding of the functional and anatomical basis of the phenomenon.

Chapter 6:

Image-based grouping during binocular rivalry is dictated by eye-of-origin

In preparation.

By Stuit, S. M., Paffen, C. L. E., van der Smagt, M. J., & Verstraten, F. A. J.

Abstract

Prolonged viewing of dichoptically presented images with different content results in perceptual alternations known as binocular rivalry. This phenomenon is thought to be the result of competition at a local level, where local rivalry zones interact to give rise to a single, global dominant percept. Certain perceived combinations that result from this local competition are known to last longer than others, which is referred to as grouping during binocular rivalry. In recent years, the phenomenon has been suggested to be the result of competition at both eye- and image-based processing levels, although the exact contribution from each level remains elusive. Here we use a paradigm designed specifically to quantify the contribution of eye- and image-based processing to grouping during rivalry. In this paradigm we used sine-wave gratings as well as upright and inverted faces, with and without binocular disparity-based occlusion. These stimuli and conditions were used because they are known to result in processing at different stages throughout the visual processing hierarchy. Specifically, more complex images were included in order to maximize the potential contribution of image-based grouping. In spite of this, our results show that increasing image complexity did not lead to an increase in the contribution of the image-based processing to grouping during rivalry. In fact, the results show that grouping was primarily affected by the eye-of-origin of the image parts, irrespective of stimulus type. We suggest that image content affects grouping during binocular rivalry at low-level processing stages, where it is intertwined with eye-of-origin information.

Introduction

During binocular rivalry, dissimilar images presented dichoptically compete for perceptual awareness. One of the primary debates in rivalry research concerns the level of processing at which this competition originates. Evidence in favour of both an early, ‘eye-based’ and a later, ‘pattern-based’ level of processing has been presented over the years (Blake, 1989; Tong & Engel, 2001; Logothetis, Leopold & Sheinberg, 1996; Silver & Logothetis, 2007). In recent years consensus seems to have been reached suggesting that rivalry competition occurs at multiple stages along the stream of visual information processing (Blake & Logothetis, 2002; Silver & Logothetis, 2007; Freeman, 2005; Lee, 2004; Nguyen, Freeman, & Alais, 2003; Wilson, 2003). In spite of this consensus, the degree to which different processing levels contribute to rivalry remains elusive. Recently, we introduced a paradigm that enables the quantification of both early (eye-based) and late (pattern-based) visual contributions to rivalry (Stuit, Paffen, van der Smagt & Verstraten, 2011).

This paradigm was based on studies showing that rivalry is the result of competition at neighbouring rivalry zones, whose competition is not independent. For example, adjacent rivalry zones tend to produce the same dominant percept when the rival targets share similar features such as motion, orientation or colour (Whittle, Bloor & Pocock, 1968; Kovács, Papathomas, Yang & Fehér, 1997; Alais & Blake 1998; Alais & Blake, 1999). In other words, different regions of images engaged in rivalry can group together during dominance, resulting in a relatively stable, long-lasting dominance period[1*]. We recently showed that this grouping of neighbouring rivalry zones is affected by at least two kinds of cues. First, the eye to which images are presented, and second, the content of the presented images (Stuit et al., 2011). Grouping based on image content results in a percept of a coherent image, whose parts are presented to different eyes. Such an effect was first reported by Diaz-Caneja in 1928 (see Alais, O’Shea, Mesana-Alais, Wilson, 2000), who presented the two halves of two coherent images (one image consisting of concentric lines and one consisting of straight lines) dichoptically, with matching halves presented to different eyes. Apart from perceiving the two different halves of the images (indicating that the input to a single eye produced the dominant percept), matching halves (i.e. concentric circles versus straight lines only) were also perceived.

[1*] The term grouping is used here to refer to the simultaneous dominance of two particular images, or image parts, presented at different spatial locations.

In other words, the two halves were grouped together in dominance to reconstruct a coherent image (also see Kovács et al., 1997). Consequently, grouping during rivalry is usually associated with grouping based on image content, thereby reflecting pattern-based, higher-level competition (Lee & Blake, 2004; Kovács, Papathomas, Yang & Fehér, 1997; Knapen, Paffen, Kanai & van Ee, 2007). However, this interpretation potentially obscures a different form of grouping, which is eye-based (e.g. perceiving the different halves of the images in Diaz-Caneja's case). In a previous study, we set out to quantify and compare this grouping based on eye-of-origin to grouping based on image content (Stuit et al., 2011).

In our previous study (Stuit et al., 2011) we used a pair of rivalling horizontal and vertical gratings. The gratings with identical orientations could be presented to the same eye or to different eyes allowing us to estimate dominance durations based on both image-content and eye-of-origin. Interestingly, grouping of images presented to the same eye appeared to be much more potent than grouping based on image-content (i.e. by orientation). The effect of a shared eye-of-origin on dominance durations was also very prominent in a second experiment using diagonally oriented gratings. In contrast, grouping based on image-content was only present for cardinally oriented gratings. Together, these results suggest that dominance duration is primarily affected by the eye-of-origin of the presented images, but that there is also room for image-based cues to contribute to grouping. Since this study (Stuit et al., 2011) only used oriented gratings, it is possible that the image-based cues where not potent enough to contribute to grouping, leading to an underestimation of the contribution of this cue. This possible pitfall is our main concern in the current study. Does the contribution of image-based grouping during rivalry increase when the image-content is biased towards images that are known to be processed relatively late in the visual processing stream?

In the first experiment of the current study we address the question whether image-based grouping increases for images that are known to be processed relatively late in the visual processing hierarchy compared to those that are processed relatively early. The feature-preferences of neurons become more complex throughout the visual processing hierarchy. While the early visual cortex shows tuning to simple orientation, later areas respond to more specific stimuli like objects (Ungerleider & Haxby, 1994), places, or faces (Kanwisher, McDermott & Chun, 1997). For example, the Fusiform Face Area (FFA) has been shown to respond preferentially to faces (Kanwisher, McDermott &

Chun, 1997). Moreover, this latter area is thought to respond to faces as a whole (Farah, Wilson, Drain & Tanaka, 1998), rather than just a collection of the parts of the face. Also, it responds preferentially to upright faces, in comparison to inverted faces (Kanwisher, Tong & Nakayama, 1998). These characteristics make faces an ideal stimulus to enhance grouping based on image content. If simultaneous dominance (i.e. grouping) is affected by higher-level face processing, we can expect a bias towards perceiving image-based grouped faces since they are processed as a whole. Alternatively, grouping during rivalry may be unaffected by such relatively late processes.

To compare image-based grouping for higher-level stimuli to stimuli processed at the lower end of the visual processing stream, we also used oriented gratings. Grouping for these kind of stimuli is known to be primarily eye-based. We also used inverted faces, as they do not activate higher-level visual processing areas as much as upright faces (Kanwisher, Tong & Nakayama, 1998).

In Experiment 2, we extent our search for higher-level influences on image-based grouping by manipulating amodal completion of our stimuli. To this end we shifted the background surrounding the rivalling items in depth to create conditions where the items appear occluded or not occluded. Relative depth can influence amodal completion by manipulating border ownership. The common border between the occluder and the object it is occluding is referred to as intrinsic to the occluder and extrinsic to the occluded object. Moreover, intrinsic borders that are part of an object are argued to hinder grouping, while extrinsic borders, which are defined by occlusion, facilitate grouping (Nakayama, Shimojo & Silverman, 1989).

Experiment 1

Methods

Participants
A total of 7 participants, including one of the authors (SS) participated in the experiment. This study involves healthy human participants, and does not utilize any invasive techniques, substance administration or psychological manipulations. Therefore, compliant with Dutch law, this study only required, and received approval from our internal faculty board (Faculty's Advisory Committee under the Medical Research (Human Subjects) Act (WMO Advisory Committee) at Utrecht University. Furthermore, this research was conducted according to the principles expressed in the Declaration of Helsinki. All participants in the experiment had provided written informed consent. In doing so, they had indicated to have read and to have agreed with both the rules regarding participation and proper (laboratory) behavior, and the researchers' commitments and privacy policy. They are also informed that they can stop participating in the experiment whenever they want to do so and that all data would be analyzed anonymously. All participants had normal or corrected to normal vision and passed a test for stereovision (TNO test for stereoscopic vision). With the exception of SS, the participants were naïve as to the purpose of the experiment.

Apparatus
Stimuli were created on an Apple - Mac Pro computer running Matlab 7.4 with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). The stimuli were presented on a linearized LaCie III 22" at 75 Hz. Participants viewed the stimuli through a mirror stereoscope. The length of the optical path was 57 cm.

Stimuli
Experiment 1 consisted of 2 parts, which were run separately. For part 1 we used grating stimuli (Experiment 1: Gratings; Figure 1A-D), for part 2 we used face stimuli (Experiment 1: Faces; Figure 1E-H). Specifically, the rivalling images consisted of horizontal and vertical sine-wave gratings or parts of faces presented to one eye, paired with plaids presented to the other eye. The gratings were presented at a Michelson contrast of 49.7% with a space-average luminance of 25 cd/m^2. The gratings had a spatial frequency of 4.1 cpd. For the parts of the neutral faces we used a male and a female taken

from the Ekman and Friesen (1976) face stimuli set. Plaids were presented at 74.4% Michelson contrast and had the same spatial frequency as the gratings. All interocular pairs were shown in circular apertures with a radius of 1.9° of visual angle whose edges were softened by a cosine ramp of 0.2° of visual angle, and were presented on a random pixel noise background of 98% (Michelson) contrast (25 cd/m^2) that was identical in both eyes. The half-images were presented within square white frames. We used four basic stimulus arrangements in our experiments (Figure 1): 1) matching images in the same hemifield – in the same eye, 2) matching images in different hemifields – in the same eye, 3) matching images in the same hemifield – in different eyes, and 4) matching images in different hemifields – in different eyes. The distance from the fixation point to the centre of the target was 2.1° of visual angle and identical for all targets in all conditions.

Procedure

Participants performed the experiment in a darkened room with their heads supported by a chin rest. Before the onset of each trial, participants were presented with two identical pixel noise half-images surrounded by white frames. At the centre of each half-image was a fixation point. When ready, an participant initiated a trial by pressing the space-bar key. Next, two gratings (either both horizontal or both vertical) or two parts of a face (upright or inverted) were presented in one of four possible spatial arrangements with two plaids in corresponding locations of the other eye. Participants performed a 3AFC perceptual tracking task where their task was to continuously indicate via a key press whether they perceived one plaid (left arrow key), two plaids (right arrow key) or no plaids (no press). Each trial lasted 45s. After each trial, the rivalling targets were removed from the screen. Participants were instructed to fixate on the fixation point throughout the experiment. The experiment typically lasted about 140 minutes and was completed in 8 blocks.

Analyses

For our main analyses we ran repeated measures ANOVAs on two data sets for both parts (grating- and face-stimuli) of the experiment: individual epoch durations and overall fraction of time a particular percept was dominant during a trial. For epoch duration we used the median of epochs per condition. This parameter is very informative about percept stability. For the fractions overall dominance we used the mean fraction per condition. Fractions are very informative about biases towards certain percepts.

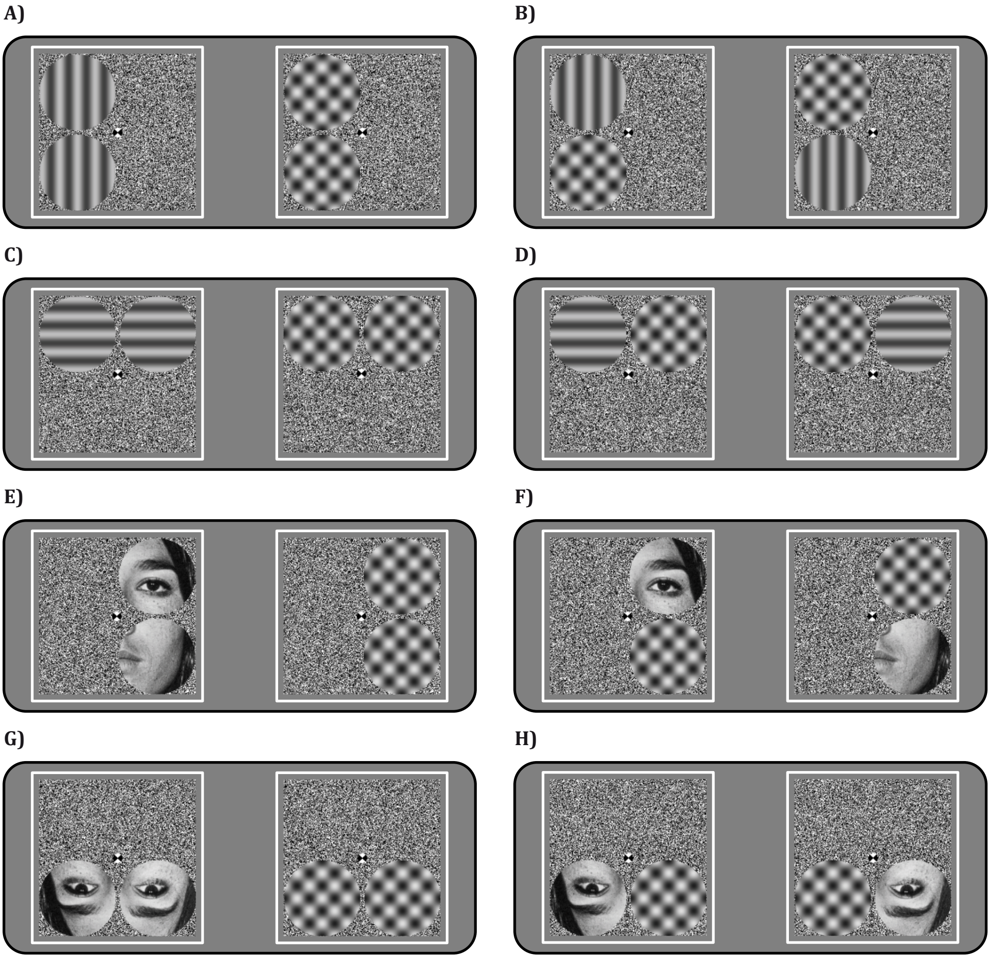


Figure 1: Schematic examples of the competing stimuli used in Experiment 1. Identical or matching images were presented in four different conditions:

1) Matching images presented to the same eye and the same hemifield (A/E).

2) Matching images presented to the same eye and in different hemifield (C/G).

3) Matching images presented to different eyes and in the same hemifield (B/F).

4) Matching images presented to different eyes and in different hemifields (D/H).

Note that, for 3AFC-paradigms, results based on epoch durations and overall fractions may differ. For example, a particular percept may last only shortly (resulting in a short epoch duration) but occur very often (resulting in a large overall fraction).

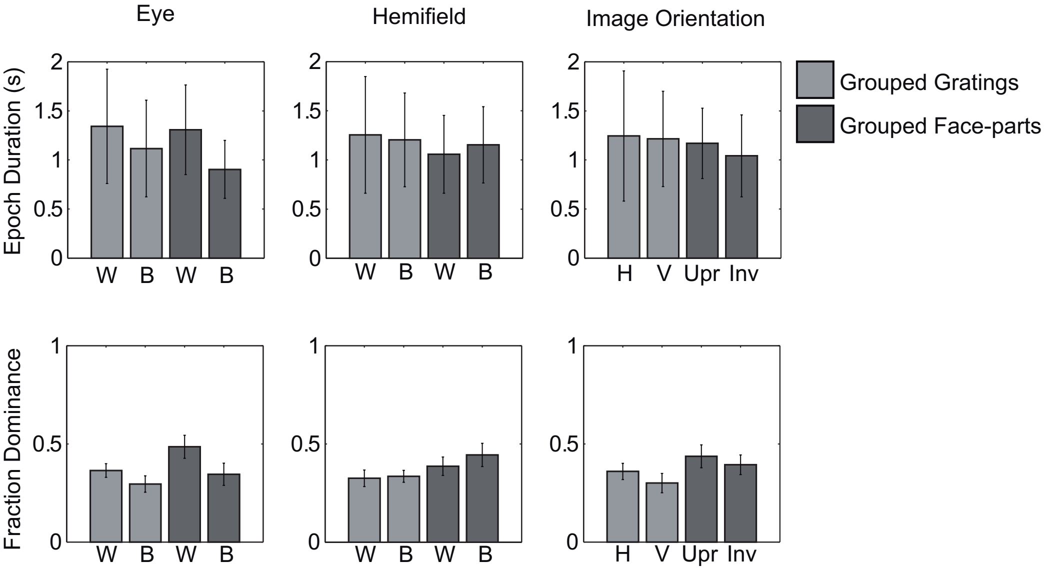
Our post-hoc planned comparisons focus on the differences between the results when using grating-stimuli and when using face-stimuli. Namely, we set out to test the differences (using paired-samples t-tests) between the average median epoch durations and the average fractions overall dominance for 1) grouped gratings and grouped faces, 2) grouped plaids in Experiment 1 and grouped plaids in Experiment 2, and 3) mixed percepts of a grating and a plaid and mixed percepts of a face-part and a plaid. These comparisons were done for both within- and between-eye dominance. We set our a to 0.0085 based on the Šidák (1967) correction to adjust for multiple (6) comparisons per data type (epoch durations and fractions overall dominance).

Results

For our analyses we extracted the median dominance epoch duration and fractions of total dominance duration for each of the three possible perceptual outcomes. When using grating-stimuli, these were responses indicating grouped gratings, grouped plaids and mixed percepts of one grating and one plaid. When using face-stimuli, these were percepts of grouped face-parts, grouped plaids and mixed percepts of one face-part and one plaid. A 2 (image orientation) x 2 (within- vs. between eye dominance) x 2 (within- vs. between hemifield dominance) repeated measures ANOVA was performed for each perceptual outcome. Tables 1 and 2 show a summary of the test statistics for grating- and face-stimuli respectively.

Importantly, only in one condition we found an effect of image-orientation (IO, mixed percept in table 2): here the combination of a plaid and an inverted face-part lasted an average of 0.17 (standard error: 0.05) seconds longer than a plaid and an upright face-part. Note that, next to small size of the effect, its direction is opposite to our hypothesis: Upright faces were assumed to results in longer dominance durations than inverted faces due to their relatively late processing locus. Except for this effect on mixed-percept durations when using face-stimuli, no main effect of image-orientation was apparent in either experiment ('IO': all perceptual outcomes in tables 1&2). This means that horizontal and vertical gratings did not differ in their epoch duration or fractions of overall dominance. Likewise, upright and inverted face-parts did not differ in their epoch duration or fractions of overall dominance either. Instead, grouping during dominance appears to be affected primarily by eye-of-origin of the dominant images (the same eye or different eyes; 'Eye', all perceptual outcomes in tables 1&2). Specifically, images that were presented to the same eye tended to be dominant together for longer periods and an overall larger proportion of time (Figure 2).

When using face-stimuli, we found main effects for the location in the visual field of the dominant images (i.e. within- versus between hemifields). For both dominant face parts and plaids, images in different hemifields resulted in longer simultaneous dominance than images in the same hemifield (Hemifield in table 2; also see Figure 2 & 3). However, for a mixed face-plaid percept, images were dominant together more within the same hemifield (Figure 3). For both grating- and face-stimuli, we mainly found interactions between the eye-of-origin of the dominant images and their placement across the visual field (IO by hemifield interaction in table 1 and table 2; also see Figure 3). Specifically, when using gratings, images presented to the same eye appeared to be dominant together longer when presented in the same hemifield, compared to different hemifields. However, when the images were presented to different eyes, they were dominant together longer when in different hemifields, compared to the same hemifield (Figure 3). These finding replicate our previous work on grouping (Stuit et al., 2011). When using face-stimuli, interactions between the arrangement across the visual field and eye-of-origin of the dominant images were also apparent (Figure 3 & 4). However, this relationship appears to be affected by the presence of a main effect how the items are arrangement across the visual field (i.e. the hemifield condition). We suggest the main hemifield effect and the hemifield by eye interaction have opposite effects on *within*-eye grouping durations for face-parts and plaids. This results in the effect of hemifield appearing smaller for within-eye dominance. For mixed face-plaid percepts, the main hemifield effect is opposite to the main hemifield effect for grouped faces and grouped plaids: for mixed percepts, within-hemifield grouping is more prominent instead of between-hemifield grouping. Now, the main hemifield effect and the hemifield by eye interaction have opposite effects on *between*-eye grouping. As a result, the effect of hemifield appears smaller for between-eye dominance (Figure 3 & 4).



***Fi**gure 2: Main effects of Experiment 1*

Overview of main effects of within- versus between eye dominance, within- versus between hemifields and image orientation for grouped gratings (light grey) and grouped face-parts (dark grey). Error bars represent the 95% confidence intervals. The 3 top panels depict the average median epoch duration in seconds. Each participant's data was normalized using his or her overall median dominance duration. After averaging across participants the averages were multiplied by the overall median across all participants, which results in a duration in seconds. Note that this normalization used was only for graphical purposes. The other 3 panels depict the fraction of overall dominance. The different conditions are denoted on the abscissa as follows W: within- eye/hemifield, B: between- eye/hemifield, H: horizontal, V: vertical, Upr: upright, Inv: Inverted.

Percept	Gratings (no response)						Plaids (2 plaids response)						Mixed (1 plaid response)					
Data type	Median			Fraction			Median			Fraction			Median			Fraction		
Statistic	F	p	$_p\eta^2$	F	p	$_p\eta^2$	F	p	$_p\eta^2$	F	p	$_p\eta^2$	F	p	$_p\eta^2$	F	p	$_p\eta^2$
Image orientation (IO)	0.04	.84	.01	5.85	>.05	.50	3.89	.10	.39	11.32	.02	.65	0.05	.83	<.01	7.45	.03	.55
Eye	4.87	.07	.45	**18.36**	**<.01**	**.75**	**10.30**	**.02**	**.63**	**27.63**	**<.01**	**.82**	**10.87**	**.02**	**.64**	**25.37**	**<.01**	**.81**
Hemifield	0.11	.75	.02	0.51	.50	.08	<0.01	.97	.00	8.69	.03	.59	4.24	.09	.41	3.93	.10	.40
IO by eye	3.92	.10	.40	2.34	.18	.28	1.79	.23	.23	0.07	.80	.01	0.54	.49	.08	0.91	.38	.12
IO by hemifield	0.85	.39	.12	2.11	.20	.26	<0.01	.96	<.01	3.30	.12	.36	0.39	.56	.06	0.33	.58	.05
Eye by hemifield	4.23	.09	.41	**49.34**	**<.01**	**.89**	4.51	.08	.43	**15.76**	**<.01**	**.72**	**12.08**	**.01**	**.70**	**38.52**	**<.01**	**.87**
IO by eye by hemifield	0.62	.64	.09	3.21	.12	.39	0.84	.39	.12	5.35	.06	.47	0.52	.50	.08	0.13	.73	.02

Table 1: A summary of the analyses of Experiment 1 when using grating-stimuli.
F- & p-values as well as the partial eta squared (Statistic) for both median durations and fractions of overall dominance (Data type) are reported for the three possible perceptual outcomes (Percept). The different comparisons are noted in the left-most column. Significant effects are printed in bold. Note that image orientation for plaids refers to the orientation of the suppressed images.

The main aim of Experiments 1 was to test whether more image-based grouping occurs when using images that are processed higher up the visual processing hierarchy (i.e. that require neural machinery beyond early visual cortex). The lack of differences in grouping upright versus inverted face-parts suggests that the proposed higher-level processing of faces does not contribute to a large extent to grouping during rivalry. However, since inverted faces can still be considered 'more complex' and therefore might still have been processed at relatively late processing stages, albeit to a lesser extent than upright faces (Kanwisher, Tong & Nakayama, 1998), we also compared faces directly to gratings. To this end, we focused on the difference between dominance durations for grouped gratings and grouped parts of faces (irrespective of grating or face orientation). Epoch durations did not differ between the grouped gratings and faces during within-eye dominance (*t(1,6) = 0.5405, p = .608*) nor during between-eye dominance (*t(1,6) = 2.1362, p = .077*; see also Figure 3). Note that the comparison of between eye-dominance of the two percepts is a direct comparison of image-based grouping, since image-complexity is the only possible source of a difference in grouping of these images.

Percept	Face (no response)						Plaids (2 plaids response)						Mixed (1 plaid response)					
Data type	Median			Fraction			Median			Fraction			Median			Fraction		
Statistic	F	p	$p\eta^2$	F	p	$p\eta^2$	F	p	$p\eta^2$	F	p	$p\eta^2$	F	p	$p\eta^2$	F	p	$p\eta^2$
Image orientation (IO)	1.51	.27	.20	5.18	.06	.46	2.42	.17	.29	3.29	.12	.35	**12.71**	**.01**	**.68**	1.74	.24	.23
Eye	**14.75**	**<.01**	**.71**	**35.87**	**<.01**	**.86**	5.32	.06	.47	**14.39**	**<.01**	**.71**	**31.43**	**<.01**	**.84**	**30.33**	**<.01**	**.84**
Hemifield	0.83	.40	.12	**11.77**	**.01**	**.66**	**13.95**	**.01**	**.70**	**15.38**	**<.01**	**.72**	**9.82**	**.02**	**.62**	**29.86**	**<.01**	**.83**
IO by eye	3.65	.11	.38	1.44	.28	.19	<.01	.98	<.01	0.87	.39	.13	1.57	.26	.21	2.62	.16	.30
IO by hemifield	0.06	.81	.01	**7.75**	**.03**	**.56**	1.32	.29	.18	0.76	.42	.11	5.68	.05	.49	7.90	.03	.57
Eye by hemifield	0.20	.67	.03	**28.58**	**<.01**	**.83**	3.89	.10	.39	**43.58**	**<.01**	**.88**	**17.58**	**<.01**	**.75**	**112.96**	**<.01**	**.95**
IO by eye by hemifield	0.01	.92	<.01	0.06	.81	.01	1.20	.32	.17	0.03	.88	<.01	2.19	.19	.27	0.17	.70	.03

Table 2: A summary of the analyses of Experiment 1 when using face-stimuli.
F- & p-values as well as the partial eta squared (Statistic) for both median durations and fractions of overall dominance (Data type) are reported for the three possible perceptual outcomes (Percept). The different comparisons are noted in the left-most column. Significant effects are printed in bold. Note that the orientation of the faces did not affect their epoch durations or the overall dominance (IO).

The results of Experiment 1 suggest a limited effect of the type of dominant images used on grouping durations. However, we did find that epoch durations of dominant plaids were shorter when face-parts, in comparison to gratings, were suppressed (*within-eye dominance: t(1,6) = 4.2748, p = .005, between-eye dominance: t(1,6) = 5.0349, p = .002*; see Figure 3). This result suggests that plaids group together better during dominance when gratings are suppressed. Alternatively, this could also suggest that face-parts are more potent in breaking suppression than gratings. In light of previous results showing shorter suppression durations for emotional faces compared to neutral faces (Alpers & Gerdes, 2007; Bannerman, Milders, De Gelder & Sahrale, 2008; Yoon, Hong, Joormann & Kang, 2009), we suggest the latter option to be more plausible. No differences were found for mixed percept epoch durations depending on the stimulus type (gratings compared to faces; *within-eye dominance: t(1,6) = 2.5884, p = .041, between-eye dominance: t(1,6) = 2.6613, p = .038*; see Figure 3).

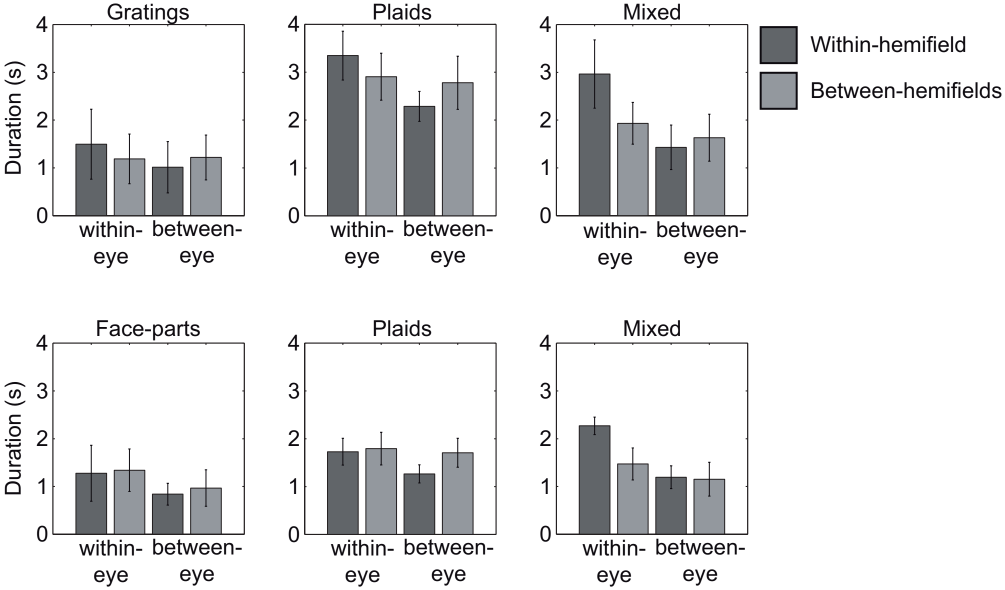


Figure 3: Median percept durations in Experiment 1.

Within-hemifield dominance durations are presented in dark grey. Between-hemifield dominance durations are presented in light grey. Error bars represent the 95% confidence intervals. For illustration purposes only, durations were normalized. Each participant's data was normalized by his or her overall median dominance duration. After averaging across participants the averages were multiplied by the overall median across all participants, which results in a duration in seconds. Note that between-eye dominance of gratings, plaids and face-parts reflects grouping based only on image-content. Within-eye dominance for mixed-percepts reflects grouping based only on eye-of-origin. Within-eye dominance for gratings, plaids and face-parts reflect a combination of eye-of-origin- and image-based grouping.

Finally, we compared the fraction of overall dominance for the different percepts when using gratings compared to using faces. Results show that grouped face-parts are perceived for a larger portion of time than grouped gratings (*within-eye dominance: t(6) = -5.7579, p = .001;* see Figure 4). Importantly, this difference was only present for within-eye dominance (*between-eye dominance: t(6) = -2.6976, p = .036;* Figure 4). This result suggests an effect of eye-of-origin on the bias towards perceiving faces as compared to gratings. Similar to the results for epoch durations, grouped plaid percepts occurred

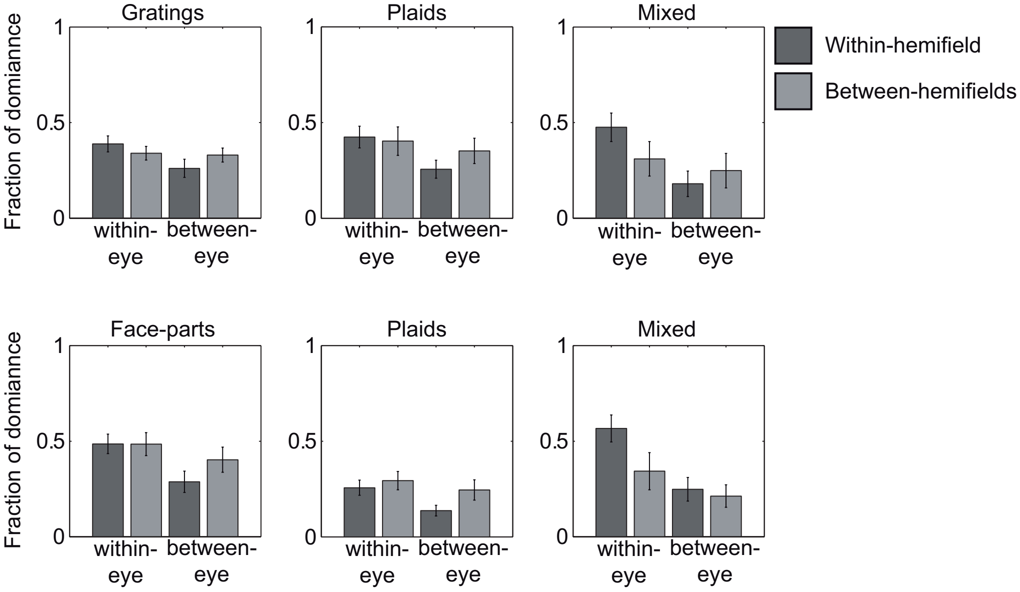


Figure 4: Fractions of overall dominance in Experiment 1.
Within-hemifield dominance durations are presented in dark grey. Between-hemifield dominance durations are presented in light grey. Error bars represent the 95% confidence intervals. Note the overall pattern in the data is similar to the epoch duration data.

for a larger portion of time when gratings are simultaneously suppressed as compared to when faces are suppressed (*within-eye dominance: t(6) = 5.9340, p = .001, between-eye dominance: t(6) = 4.1099, p = .006*; Figure 4). No differences were found between the overall occurrences of mixed percepts between the two experiments (*within-eye dominance: t(6) = -0.5809, p = .582, between-eye dominance: t(6) = -1.7484, p = .131*; see Figure 4).

Taken together, these results suggest that grouping during binocular rivalry dominance is primarily affected by the source, that is the eye-of-origin, and the relative positions in the visual field of the grouped images. Grouping is not different for higher-level image modulations such as face-inversion. We did, however, find a difference between the overall durations for perceiving grouped faces and perceiving grouped gratings. Importantly, this effect was only present for within-eye dominance, showing that different image content can increase the overall duration of eye-based dominance.

Experiment 2

In Experiment 1 we did not observe an increase in image-based grouping for upright faces when comparing them to inverted faces. Nor was such an increase apparent when individual epoch durations between faces and gratings were compared. In contrast, a shared eye-of-origin resulted in more grouping during dominance for all percepts. Note that this finding is in line with the results from our previous work (Stuit et al., 2011). We also found variations in dominance durations based on differences in the arrangement across the visual field, and again these effects concur with our previous findings.

In the next experiment we will explore a different approach to test for an increase in the contribution of image-based grouping. We will use depth cues to manipulate amodal completion; when an object is occluded by another object, the occluded object's shape can be amodally completed without sensory input (Palmer, Neff & Beck, 1996). Relative depth can have a profound effect on amodal completion by manipulating border ownership (Nakayama, Shimojo & Silverman, 1989). The common border between the occluder and the occluded object is referred to as *intrinsic* to the occluder and *extrinsic* to the occluded object. Moreover, borders considered intrinsic to an object are argued to hinder grouping, while extrinsic borders facilitate grouping (Nakayama, Shimojo & Silverman, 1989). Here we use the relative depth of the surrounding background and the rivalling items to create conditions where the items appear occluded or non-occluded, by shifting the background in depth toward or away from the observer. We expected that manipulating amodal completion with border ownership would affect image-based grouping specifically since eye-based grouping is thought to be unaffected by image-content (Stuit et al., 2011). Moreover, if amodal completion facilitates image-based grouping, the effect may be largest for upright faces. That is, as compared to gratings and inverted faces, since this stimulus is considered to be the most complex, and requires high-level image-based processing.

Methods

Participants

10 participants, including 3 participants from the previous experiment, participated in Experiment 2. This study involves healthy human participants, and does not utilize any invasive techniques, substance administration or psychological manipulations. Therefore, compliant with Dutch law, this study only required, and received approval from our internal faculty board (Faculty's Advisory Committee under the Medical Research (Human Subjects) Act (WMO Advisory Committee) at Utrecht University. Furthermore, this research was conducted according to the principles expressed in the Declaration of Helsinki. All participants in the experiment had provided written informed consent. In doing so, they had indicated to have read and to have agreed with both the rules regarding participation and proper (laboratory) behavior, and the researchers' commitments and privacy policy. They are also informed that they can stop participating in the experiment whenever they want to do so and that all data would be analyzed anonymously. All had normal or corrected to normal vision and all but one were naïve as to the purpose of the study. Again, all participants passed a test for stereo-vision and provide informed consent before participating.

Apparatus

The materials and software used were identical to Experiment 1.

Stimuli & Procedure

The stimuli and procedure used in Experiment 2 were identical to those used in the first experiment, with the following exceptions: All stimuli were presented along the vertical meridian (see Figure 5). The hemifield condition was removed to focus solely on eye- and image-based contributions. For the noise-background we used band-pas filtered pixel noise. The background was presented with a crossed and uncrossed disparity of 10 min/arc to achieve the percept of occluded or non-occluded rivalling images. To keep the task focused on the plaids, we now included a 'zeros-plaids-visible' response button. This response button was added to remove a potential bias towards percepts that contained plaids. Participants thus used 3 keys in the perceptual tracking task instead of 2. Furthermore, trials lasted 60s instead of 45s, making the total duration of Experiment 2 identical to Experiment 1.

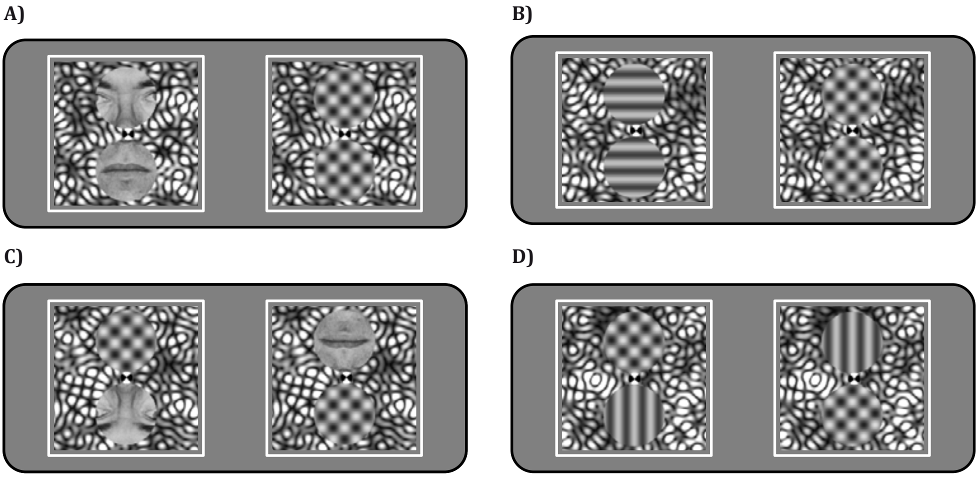


Figure 5: Schematic representation of the stimuli used in Experiment 2.
Matching images were presented along the vertical meridian and could be presented to the same eye (A&B) or to different eyes (C&D). For the matching images we used upright (A) and inverted (C) faces, as well as vertical (B) and horizontal gratings (D). The surround was presented with either crossed or uncrossed disparity, resulting in the images being perceived as either being occluded by the surround or not.

Results

*F*or our analyses we extracted the median dominance epoch durations and fractions of total dominance duration for each of the possible perceptual outcomes. A 2 (occluded versus not occluded) x 2 (image orientation) x 2 (within- versus between eye dominance) repeated measures ANOVA was performed for each percept. That is, grouped face-parts or gratings, grouped plaids and mixed percepts of one face-part or grating and one plaid. The statistical results are summarized in table 3 (for grating-stimuli) and table 4 (for face-stimuli). We found neither a main effect of occlusion, nor any interactions between occlusion and any other condition on grouping during rivalry dominance (Occlusion, Occlusion by IO, Occlusion by eye & Occlusion by IO by eye in tables 3 and 4; Figure 6 upper and lower middle panels). This result suggests that amodal completion does not affect grouping during rivalry dominance. However, within-eye dominance resulted in longer epoch durations and more overall dominance than between-eye dominance for all percepts (Eye in tables 3 and 4; figures 7 and 8). As was true for the first two experiments, these results show a bias towards perceiving images presented to the same eye. These images are grouped together longer at the level of individual epochs as well as have longer overall durations (see figures 7 and 8).

In contrast to Experiment 1, in Experiment 2 we *do* find a significant difference between the fractions of dominance for upright versus inverted faces (IO in table 4). This difference reflects a small bias toward perceiving upright face-parts compared to inverted face-parts (Figure 6, upper right panel). This bias is apparent for 9 out of 10 participants, but the magnitude was limited to a difference between fractions of 0.024 (standard error of the difference: 0.007). At the level of individual epoch durations, however, the upright face-parts were not perceived for longer consecutive periods than the inverted face-parts.

In post-hoc comparisons, we compared the medians of individual epoch durations between using grating- and face-stimuli (see Figure 7), using the same planned comparisons as for Experiments 1. We found no differences between epoch durations for grouped faces compared to gratings (*within-eye dominance: t(9) = 2.5401, p = .032; between-eye dominance: t(9) = -0.2882, p = .779*). The epoch durations for grouped plaids when using gratings did also not differ from the epoch durations for grouped plaids when using faces (*within-eye dominance: t(9) = -1.4667, p = .176; between-eye*

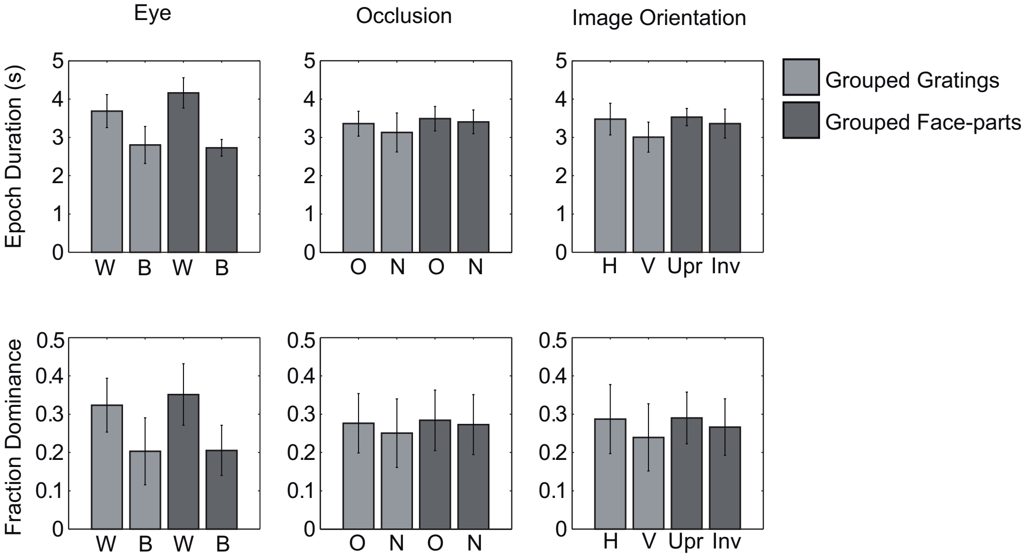


Figure 6: Main effects of Experiment 2.

Overview of main effects for within- versus between eye dominance, occluded versus not occluded and image orientation for grouped gratings (light grey) and grouped face-parts (dark grey). Error bars represent 95% confidence intervals. The top three panels depict the average median epoch duration for grouped gratings (light grey) and grouped face-parts (dark grey). Each participant's data was normalized using his or her overall median dominance duration. After averaging across participants the averages were multiplied by the overall median across all participants, which resulted in a duration in seconds. Note that the data normalization was for graphical purposes only since we used a within-subjects statistical design. The bottom three panels depict the fractions of overall dominance for grouped gratings and grouped face-parts. The different conditions are denoted on the abscissa as follows: W: within-eye, B: between-eyes, O: occluded, N: not occluded, H: horizontal, V: vertical, Upr: upright, Inv: Inverted. Note that between-eye grouping (left panels, conditions B) reflects grouping based on image-content only.

Percept	Gratings (0 plaid response)						Plaids (2 plaids response)						Mixed (1 plaid response)					
Data type	Median			Fraction			Median			Fraction			Median			Fraction		
Statistic	F	p	$_p\eta^2$	F	p	$_p\eta^2$	F	p	$_p\eta^2$	F	p	$_p\eta^2$	F	p	$_p\eta^2$	F	p	$_p\eta^2$
Occlusion	0.86	.38	.09	1.07	.33	.11	0.94	.36	.10	0.03	.87	<.01	0.04	.85	>.01	0.48	.51	.05
Image orientation (IO)	4.30	.07	.32	2.35	.16	.21	0.20	.66	.02	1.58	.24	.15	0.04	.85	>.01	<.01	.93	<.01
Eye	**7.52**	**.02**	**.46**	**42.72**	**<.01**	**.83**	**14.35**	**<.01**	**.62**	**30.98**	**<.01**	**.78**	**16.78**	**<.01**	**.65**	**39.40**	**<.01**	**.81**
Occlusion by IO	1.94	.20	.18	3.02	.12	.25	<.01	.95	<.01	0.22	.65	.02	1.99	.19	.18	0.57	.47	.06
Occlusion by eye	0.04	.85	<.01	1.03	.34	.10	1.27	.29	.12	3.05	.12	.25	0.50	.50	.05	4.70	.06	.34
IO by eye	2.04	.19	.19	0.34	.57	.04	0.11	.75	.01	1.08	.33	.11	0.30	.60	.03	0.36	.56	.04
Occlusion by IO by eye	0.26	.62	.62	2.71	.13	.23	1.00	.34	.10	1.54	.25	.15	0.40	.55	.04	<.01	.99	<.01

Table 3: A summary of the analyses results of Experiment 2 when using gratings.
F- and p-values as well as the partial eta squared (Statistic) for both median durations and fractions of overall dominance (Data type) are reported for the three possible perceptual outcomes (Percept). The different comparisons are noted in the left-most column. Significant effects are printed in bold. Note that significant differences are only present between within- and between-eye dominance.

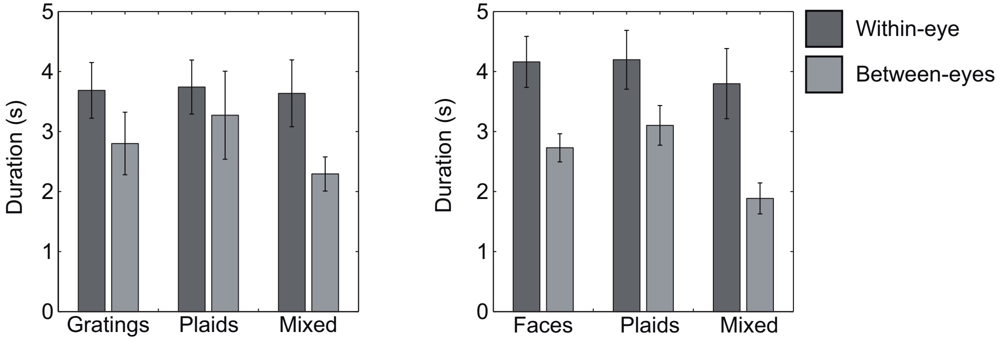


Figure 7: Median percept durations for Experiment 2.
Within-eye dominance durations are presented in dark grey. Between-eye dominance durations are presented in light grey. Error bars represent the 95% confidence intervals. For graphical purposes the data was normalized by each participant's overall median duration before being averaged across subjects and then multiplied by the overall median across all participants. Note the strong dependency on the eye-of-origin of the dominant images.

Percept	Face (0 plaid response)						Plaids (2 plaids response)						Mixed (1 plaid response)					
Data type	Median			Fraction			Median			Fraction			Median			Fraction		
Statistic	F	p	$p\eta^2$	F	p	$p\eta^2$	F	p	$p\eta^2$	F	p	$p\eta^2$	F	p	$p\eta^2$	F	p	$p\eta^2$
Occlusion	0.49	.50	.05	0.24	.64	.03	0.02	.90	<.01	1.01	.34	.10	2.49	.15	.22	0.70	.42	.07
Image orientation (IO)	0.72	.42	.07	**10.74**	**.01**	.54	0.65	.44	.07	0.38	.55	.04	0.85	.38	.09	1.30	.28	.13
Eye	**58.29**	**<.01**	**.87**	**106.30**	**<.01**	**.92**	**18.14**	**<.01**	**.67**	**40.91**	**<.01**	**.82**	**53.55**	**<.01**	**.87**	**167.02**	**<.01**	**.95**
Occlusion by IO	0.25	.63	.03	0.26	.62	.03	0.18	.68	.02	0.64	.45	.07	0.39	.55	.04	0.97	.35	.10
Occlusion by eye	<.01	.99	<.01	0.07	.80	<.01	0.02	.90	<.01	0.39	.55	.04	1.34	.28	.13	0.45	.52	.05
IO by eye	0.85	.38	.09	2.30	.60	.03	0.60	.46	.06	2.10	.18	.19	0.01	.91	<.01	2.60	.14	.22
Occlusion by IO by eye	0.48	.51	.05	0.04	.84	<.01	0.31	.59	.03	0.22	.65	.02	0.35	.57	.04	<.01	.93	<.01

Table 4: A summary of the analyses of Experiment 2 when using faces.
F- and p-values as well as the partial eta squared (Statistic) for both median durations and fractions of overall dominance (Data type) are reported for the three possible perceptual outcomes (Percept). The different comparisons are noted in the left-most column. Significant effects are printed in bold. Note that the most common significant effects are between within- and between-eye dominance.

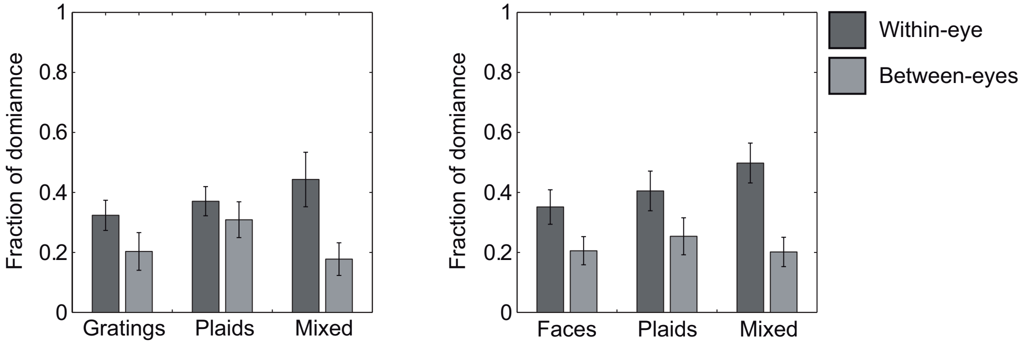


Figure 8: Fractions of overall dominance for Experiment 2.
Within-eye dominance is presented in dark grey. Between-eye dominance is presented in light grey. Error bars represent the 95% confidence intervals. Note that the dependency on the source (i.e. the eye-of-origin) of the dominant images is similar to the epoch duration data.

dominance: t(9) = - 0.4399, p = .670). Likewise, epoch durations for mixed percepts did not differ depending on the stimuli used (gratings compared to faces; *within-eye dominance: t(9) = -0.5766, p = .578; between-eye dominance: t(9) = 2.9835, p = .015*).

Next, we compared the fractions of overall duration for grouped faces to those of grouping oriented gratings (Figure 8). Contrary to the comparisons between the results for the first experiment, there was no difference between the fractions of overall durations for gratings and faces (*within-eye dominance: t(9) = 0.8761, p = .404; between-eye dominance: t(9) = 0.0802, p = .938*). These results suggest that there is no difference between the occurrence of grouping gratings and faces. Also in contrast to Experiment 1, we did not find any difference in the durations for grouping plaids (*within-eye dominance: t(9) = -1.0896, p = .304; between-eye dominance: t(9) = 1.7034, p = .123*). Apparently, the increased duration for dominant plaids that depended on the suppressed image is not consistent across experiments. Our final comparison showed no differences between mixed-percept durations when using faces compared to gratings (*within-eye dominance: t(9) = -2.2665, p = .049; between-eye dominance: t(9) = -1.3419, p = .213*). These results do not indicate any higher-level involvement in grouping during rivalry.

General Discussion

In the current study we investigated whether complex images that require processing at relatively late stages of the visual hierarchy increase the potential of image-based grouping during binocular rivalry. Our previous results demonstrated that image-based grouping can essentially be reduced to zero, while eye-based grouping remains strong when grating stimuli are used (Stuit et al., 2001). Specifically, in that study, we found an increase in dominance durations based image-content for cardinally oriented gratings, but not for diagonally oriented gratings. However, the images used in that experiment always consisted of simple gratings, which are already well processed in early visual areas. To overcome this possible limitation, we now also used parts of faces, either upright or inverted. Moreover, the competing images were presented with and without disparity-based occlusion. Using images that are believed to rely on later processing stages (such as the IT complex; Kanwisher, McDermott & Chun, 1997) as well as disparity-based occlusion (resulting in amodal completion, Palmer, Neff & Beck, 1996) may promote perceptual grouping through maximizing the efficacy of image-based grouping. Despite this clear distinction between low and higher stages of visual processing, our results do not show any trace of a higher-level form of image-based grouping. Instead, the durations of grouping during rivalry remain relatively stable under most conditions and appear mostly driven by eye-of-origin.

Although image-based grouping did not show any strong influences on dominance during rivalry in our experiments, we did find several subtle indications of influences of image content on grouping during rivalry. First of all, grouped face-parts were perceived for a larger portion of time than grouped gratings. Yet, dominance durations did not differ between grouped gratings and faces, suggesting that a percept based on grouped faces occurred more often, but did not last, on average, longer than a percept of grouped gratings. Interestingly, this bias towards grouped face percepts occurred only for face parts that were presented to the *same* eye. Thus, even when image-based grouping was present, it still appeared to be driven, or at least enabled, by eye-of-origin.

A similar dependency on early visual processing in the dominance of higher-level images has been demonstrated for the transitions during rivalry (Arnold, James & Rosenboom, 2009). Arnold and his colleagues found that the spread of a transition during rivalry was slower when different facial regions were presented to different eyes. This suggests the involvement of monocular channels even for the dominance of higher-level images. A second consistent finding in our results is the modulation of grouping by the arrangement of stimuli across the visual field (as measured by overall occurrence as well as epoch durations). These results replicate our previous findings. For a full discussion on hemi-field effects on grouping during rivalry, see Stuit et al., (2011). For now, it is important to note that the pattern in the hemi-field by eye-of-origin interaction is compatible with early visual processing.

When competing images were presented at a depth level that differed from the surround (Experiment 2), we found a small bias for perceiving mixed percepts containing upright face-parts compared to inverted face-parts. It is tempting to suggest that the presence of this face-inversion effect is due to the face-parts in Experiment 2 being presented along the vertical meridian, since no such effect of face-inversion was apparent in the first experiment. However, note that the difference in fraction dominance was very small (Fraction upright faces; average: 0.29, standard error: 0.02, Fraction inverted faces; average: 0.27, standard error: 0.02) and that we did not find any differences at the level of epoch durations for dominant faces. This shows that the effect of face inversion is not very robust. However, grouped faces were *not* dominant longer than grouped gratings for Experiment 2. Still, there was a trend of more overall grouping for faces relative to gratings. Yet, and again, this trend was only present during the eye-based grouping of faces. Therefore, we suggest an eye-level dependency for an effect that would previously have been attributed to higher-level processing (Kovács, Papathomas, Yang & Fehér, 1996).

Overall, our results show that the duration of and bias towards grouping during rivalry dominance is primarily determined by the eye-of-origin of the images. Still, image-content does undeniably play a role in grouping during rivalry, as is apparent from our own results (Stuit et al., 2011) as well as the results of others (e.g. Whittle, Bloor & Pocock, 1968; Kovács, Papathomas, Yang & Fehér, 1996; Alais & Blake 1998). It is important to note, however, that results showing interocular grouping (simultaneous dominance of matched images presented to different eyes) have been used previously to state that dominance *cannot* be explained on a level of ocular dominance columns (Kovács et al., 1996). Nevertheless, the rivalling images, as well as the distance between them, tend to be relatively small in these experiments. This is also true for our own studies on grouping. This allows for explanations based on low-level lateral connections or effects based on the extra-classical receptive field since the rivalling elements should be processed relative close to each other in retinotopic coordinates. For example, Tong, Meng and Blake (2006) have suggested a model of binocular rivalry that includes feedback from a pattern-level of processing to a monocular level of processing. Importantly, they have also included lateral connections to account for a low-level, monocular version of image-based grouping. This latter component is similar to what is suggested from our data (also see Stuit et al., 2011).

On the other hand, grouping during rivalry may not be established by early visual processing directly. Instead, dominance during rivalry, including grouped percepts, may involve higher-level brain structures that may modulate activity in lower-level structures by means of feedback (Arnold, James & Rosenboom, 2009; Tong, Meng & Blake, 2006). However, we suggest that the contribution of feedback on grouping is probably much smaller than the contribution from these lateral connections. Moreover, based on our observation that image-based grouping is mostly absent in our study, it may even be that feedback is absent, at least in the conditions tested here. The differences in grouping durations for different combinations of images, might even reflect grouping on the basis of their low-level features, rather than a higher-level modulation.

Our results imply that image-based grouping is intertwined with eye-based grouping effects. We believe this reflects an early, monocular, processing stage for grouping during rivalry. The most straightforward source for this involvement is the ocular dominance columns in the early visual cortex. This is clearly not necessarily incompatible with image-based grouping with features such as orientation (Alais & Blake 1998; Alais & Blake, 1999). Neurons within ocular-dominance columns are not only tuned to eye-of-origin but also to orientation and to spatial frequency (among others). This means they code different image aspects as well as the source of the image (Hubel & Wiesel, 1974; Hubel & Wiesel, 1962, De Valois, Yund & Hepler, 1982). These columns may thus have all the machinery necessary for both the eye- and image-based grouping effects reported here. Theoretically, this would place image- and eye-based grouping during rivalry dominance at the same level of processing.

In summary, we have presented a large set of results on grouping during rivalry dominance that can be combined into a straightforward conclusion; grouping during rivalry is primarily based on low-level, early visual features such as orientation. A persistent pattern in our results is the importance of the eye-of-origin aspect of grouping during rivalry. Image content (i.e. its feature content) does play a role in grouping but that it exerts its influence on a low level of the visual hierarchy, where it is intertwined with eye-of-origin information.

Acknowledgments

We would like to thank Margo Kocken for her contribution to the data collection for the reported experiments.

Chapter 7:

Summary and Discussion

In this thesis we aimed to elucidate the interactions between visual information of which observers are aware, versus that of which they are unaware. These interactions were investigated under conditions of binocular rivalry. On the one hand, the focus was on a local scale, i.e., the interaction between the processing of isolated competing images. On the other hand, we also investigated the interaction between multiple, spatially separated competing images, reflecting interaction on a global scale. We set out to answer the following questions:

- *Does the degree of suppression of image features depend on the content of the rivalling images?*
- *Is sensitivity to image features during dominance the same as during monocular viewing?*
- *In what way are dominant images affected by suppressed images?*
- *Is the origin of perceptual alternations affected by local variation in suppressed images?*
- *What are the relative contributions of eye- and image-based processing to binocular rivalry?*
- *Does the contribution of eye- and image-based processing vary as a function of image complexity?*

Before we discuss the answers to these questions and their implications, the main results of this thesis are summarized.

The nature of rivalry suppression was investigated in Chapter 2. Previous studies on rivalry suppression have led to controversies concerning the nature and extent of suppression during binocular rivalry. We tested for feature-specific suppression using orthogonal rivalling gratings and measuring contrast sensitivity for small grating probes with a range of orientations added to one of the images in a 2AFC orientation discrimination task. Results indicate that suppression is not uniform across orientations: suppression was much stronger for orientations within a narrow range around the orientation of the suppressed rival grating, with a tuning similar reminiscent of orientation bandwidths found in V1 neurons (Hubel & Wiesel, 1962, De Valois, Yund & Hepler, 1982). A similar experiment that assessed spatial frequency tuning demonstrated that suppression was stronger for frequencies close to that of the suppressed grating. The results imply that rivalry suppression cannot be a non-selective process.

Interestingly, suppression did not appear tuned to orientation when a flicker-and-swap paradigm (Logothetis et al., 1996) was used, suggesting that the tuning of suppression is related to, or at least strongest for, lower-level, eye-based rivalry. Together, the results suggest that there are two components to rivalry suppression: a general feature-invariant component and an additional component specifically tuned to the rivalling features.

The influence of suppressed images on the perception of dominant images was investigated in Chapter 3. It has been argued that perception during the dominance phase of rivalry is unaffected by the suppressed image (Tsuchiya, Koch, Gilroy & Blake, 2006; Alais & Blake, 2005; Gilroy & Blake, 2004). Recent evidence suggests, however, that the suppressed image *does* affect perception of the dominant image (Carlson & He, 2000; Pearson & Clifford, 2005), yet the extent and nature of this interaction remained elusive. We hypothesized that this interaction depends critically on the difference in feature content between the rivalling images. We investigated how sensitivity to probes, presented in the perceptually dominant image, is affected by the content of the suppressed image. Observers performed a 2AFC discrimination task on oriented probes and probes with different motion directions.

The results show that sensitivity to probes in dominant images appears to be strongly affected by the feature content of the suppressed image. This means that binocular rivalry dominance is not identical to viewing a stimulus with one eye only. Instead, an image that is suppressed from awareness during rivalry affects the perceptually dominant image as if it were visible as well. The similarity between these findings and our previous results on selectivity during suppression suggests that the selective component of binocular rivalry competition not only affects suppressed visual information but dominant visual information as well.

The selective nature of suppression was used to test whether this selectivity also influences the transitions during rivalry in Chapter 4. With larger images, such perceptual alternations will typically start locally and then gradually spread across the image, known as travelling waves of perceptual dominance. Several image-features (such as local contrast) are known to determine where in the image a travelling wave originates. We specifically investigated whether orientation contrast in the suppressed image affects these spatial origin(s) of perceptual alternations.

The spatial origin of transitions from suppressed to dominant images was found to be biased towards locations of greatest orientation contrast. This increase in bias appears related to the efficiency of visual search for the orientation contrast, as tested offline: we found large biases towards orientation contrast for 'efficient' visual search, and small biases for 'inefficient' search. These results show that suppression is not homogenous across the suppressed image. Instead, suppression varies across space depending on local image differences. The relation between these image differences and suppression is reminiscent of the *selective suppression* described in Chapters 2 and 3.

In Chapter 5 we investigated the spatial interactions when multiple, separate images are engaged in binocular rivalry simultaneously. Although rivalry is a local phenomenon, local rivalry gives rise to a single, global, percept. In fact, certain perceived combinations that result from this local competition last longer than others. This is generally referred to as grouping during rivalry. A paradigm was used that enabled us to separate the influence of eye-based and image-based grouping cues on simultaneous dominance of two pairs of rival images presented at different locations. Specifically, we investigated the amount of grouping during rivalry dominance and estimated the dependency of grouping durations on the source of the grouped images (to which eye the dominant image was presented) and the image-content of the dominant images (if content of the dominant images was related or unrelated).

'Eye-of-origin' was found to be the strongest cue for grouping during binocular rivalry. In addition, grouping was affected by grating orientation: identical gratings were grouped longer than gratings with dissimilar orientation, even when presented to different eyes. Our results suggest that eye-based and image-based grouping provide independent cues, whose effects are additive in nature. Grouping effects were further modulated by the distribution of the targets across the visual field. That is, grouping separated images within the same hemifield can be stronger or weaker than between hemifields, depending on the eye-of-origin of the images. These results enabled us to quantify the contribution of the different factors to grouping two images during binocular rivalry. A graphical representation of this quantification can be found on page 95 (Chapter 5, Figure 6).

In Chapter 6 the paradigm developed in Chapter 5 was used to investigate whether the extent to which eye- and image-based cues affect grouping during rivalry dominance can be manipulated by varying the complexity of the rival images. Here, stimuli containing rivalling gratings as well as upright and inverted faces, either with or without disparity-based occlusion, were used. These images and conditions are thought to result in processing at stages high up the visual processing hierarchy.

We found, however, no consistent difference in grouping based either on the orientation of faces, on occluded or non-occluded images pairs, nor did we find any consistent differences in the amount of image-based grouping between grating and face stimuli. In fact, the results show that grouping in these experiments was primarily driven by the eye-of-origin of the images. Image content does play a role in grouping but appears to be limited to the image’s basic components, which are processed at early visual processing stages (i.e. primary visual cortex). These results suggest that higher-level image processing plays only a minor role in grouping during rivalry.

Feature specificity during binocular rivalry

A key result of the present thesis is that suppression during binocular rivalry is *feature-selective*. Therefore, our discussion will start with an in-depth evaluation of this result and its implications.

Why are interactions during binocular rivalry selective to the feature-differences between the competing images? As discussed in Chapter 1 of this thesis, neurons processing similar features are located closer together in early visual cortex (Das & Gilbert, 1995). This results in stronger connections between those features (Bosking, Zhang, Schofield & Fitzpatrick, 1997). Even more so, neurons processing similar features tend to have more connections (Dalva, Weliky & Katz, 1997; Buzas, Eysel, Adorjan & Kisvarday, 2001). In line with this architecture, and in correspondence with our hypothesis, suppression was found to be strongest for image-differences for which connections are found to be both short and abundant.

Plotting the full range of suppression magnitudes in relation to relative orientation results in a tuning curve of suppression depth. The Gaussian profile of this curve, with its specific bandwidth, is informative about the level of possessing the result can be attributed to. Orientation tuning is a hallmark property of early visual processing areas

(Hubel & Wiesel, 1962; Blakemore & Campbell, 1969). Specifically, area V1 is the first brain area in humans that shows orientation selectivity, with its narrowest bandwidths of tuning being ~3° at full width of half maximum (FWHM; Hubel & Wiesel, 1962, De Valois, Yund & Hepler, 1982). In contrast, the median FWHM bandwidth of orientation selective neurons in area V4 is 52° (compared to 21° in V1) and the narrowest FWHM bandwidth recorded in V4 is 25° (compared to 3° in V1; Desimone, Schein, Moran & Ungerleider, 1985; De Valois, Yund & Hepler, 1982). Note that the bandwidth of V1 fits well with the parameters presented in Chapter 2: orientation tuning bandwidths of suppression were 26° at FWHM.

At higher levels of visual processing, neurons appear to be tuned to more complex visual features such as shape (Bruce, Desimone & Gross, 1981), and coherent motion (Rodman & Albright, 1987), while orientation selectivity becomes less prominent. For example, 40% of the neurons recorded in area IT by Desimone, Albrecht, Gross and Bruce (1984) did not show any orientation selectivity at all. The remainder of neurons showed very little orientation preference and the authors did not imply any orientation tuning for this area. IT neurons did, however, respond to more complex features such as shape. These findings show that orientation tuning becomes broader and less specific throughout the visual processing hierarchy. Importantly, these findings also show that the tuning widths found during suppression are unlikely to result from the later stages of the visual processing hierarchy.

The multiple stages of rivalry

So far, our findings suggest that rivalry competition occurs at a relatively early stage of processing. However, the current consensus is that rivalry occurs at multiple stages of the visual processing hierarchy. Although these stages are not made explicit, an eye-level (Blake, 1989) and an image/pattern-level (Logothetis et al., 1996; Kovács et al., 1996) of processing have been indicated. Note that an eye-level indicates the involvement of monocular channels, while an image/pattern-level does not. In line with this dichotomy, we have found an untuned, as well as a tuned component to rivalry suppression (Chapter 2). However, as argued in the preceding paragraphs, even tuned suppression can be implemented at the monocular level of V1. Note that V1 contains monocular channels (Hubel & Wiesel, 1962; Hubel & Wiesel, 1974).

Grouping during rivalry offers a different perspective to the issue of multiple rivalry stages. Specifically, the spatial dependencies of rivalry dominance can also be divided into contributions from both an eye- and image- components. Interestingly, results on grouping during rivalry have been used to state that dominance cannot be explained on a level of ocular dominance columns (i.e. on a monocular level; Kovács et al., 1996).

The results of our grouping experiments show that spatially separated rivalling images are dominant together for the longest periods when the images are presented to the same eye. Importantly, this does not imply that grouping is unaffected by image-content: image-content does indeed play a role in grouping during rivalry in our results, as well as in the results of other studies (Whittle, Bloor & Pocock, 1968; Kovács, et al., 1996; Alais & Blake 1998). However, because monocular channels already code for image characteristics such as orientation and spatial frequency, it is of prime importance to know which image characteristics do, and which do not, affect grouping. In other words, since eye-based information simultaneously codes for part of the image-content, which image-content *does* and which *does not* influence rivalry is important in the discussion of the level of processing required for the known grouping effects. We have put forward a restriction to the claim that higher-level, pattern-based processing is required for grouping; increasing higher-level image-content (i.e. introducing more, and more complex features) does not appear to increase the contribution of image-based grouping during binocular rivalry. In contrast, our findings show that higher-level images, such as faces and images involving amodal completion, do *not* lead to stronger image-based grouping. In fact, we suggest that image-based grouping is only based on the image-content coded at the level of the early visual cortex. For instance, orientation content of the images *does* affect the durations of simultaneous dominance during rivalry. As noted above, orientation processing is already present in early visual cortex. As such, there is no reason to assume that grouping during rivalry occurs at a relatively late stage of visual processing.

The monocular stages of rivalry

So far we have argued that eye- and image-based contributions to rivalry appear entwined since processing at the eye-level already codes for multiple aspects of image-content. Moreover, our results discussed so far do not require any involvement of a higher-, pattern-level of processing. However, we stress that we do not claim that binocular rivalry is fully resolved at the level of primary visual cortex (V1). To illustrate, we also found tuning based on coherent motion direction over a range of 180 degrees. This cannot be explained by local motion sensitivity in V1 (Snowden, Treue, Erickson & Anderson, 1991; Braddick, O'Brien, Wattum-Bell, Atkinson & Turner, 2000) and suggests at least a second stage where interactions during rivalry occur. The most likely candidate for this stage is the human analogue of area MT (hMT). This area is specialized in processing coherent motion. Importantly, recent evidence suggests that eye-of-origin information is still present at the level of hMT (Rokers, Czuba, Cormack & Huk, 2011). We suggest that access to monocular information, be it in V1, MT or other areas, is crucial for binocular rivalry.

Outstanding issues

In the preceding sections we have argued that interactions during binocular rivalry are selective to the image-content of the competing images at a monocular level. Although rivalry is thought to occur at multiple stages of the visual processing hierarchy, we have argued that any stage that involves rivalry interactions must have access to monocular information. Below we outline three issues, to be addressed in future research, that follow from the conclusions of this thesis.

1 The source versus the consequence of rivalry

We have already covered the theoretical stages of rivalry: Eye-based monocular on the one side and image/pattern-based binocular on the other. Imaging studies as well as single-unit recordings have provided many different results, which lead to many different interpretations that cannot be easily reconciled (for reviews see Blake & Logothetis, 2002 and Logothetis, 1998). Many of these studies report brain activity changes correlated with changes in the dominant percept during rivalry. Such changes are very informative of the neural correlates of awareness. However, it is important to note that strong modulations in a given area, based on the dominant percept during rivalry, is *not* informative of the source of rivalry conflict per se. In other words, strong modulations are related to awareness, not the sites involved in rivalry competition. A strong control condition can overcome some of these difficulties (Knapen, Brascamp, Pearson, van Ee & Blake, 2011). To further increase our understanding, the inhibitory mechanisms involved in rivalry suppression need to be either identified (for example: Tong & Engel, 2001; Sengpiel & Vorobyov, 2005) or their presence falsified. If rivalry indeed occurs at multiple stages throughout the visual processing hierarchy, inhibitory mechanisms whose activity correlates with rivalry suppression should be found at numerous sites.

2 A higher-level involvement in rivalry

Dominance during rivalry, including grouped percepts, may involve higher-level brain structures that modulate activity in lower-level structures (Arnold, James & Rosenboom, 2009). From this perspective, our results on grouping during rivalry can be interpreted to suggest that modulation from later processing stages is relatively weak or ineffective. Tong, Meng and Blake (2006) have suggested a model of binocular rivalry that includes feedback from a pattern-level of processing to a monocular level of processing. They have also included local lateral connections to account for a low-level, monocular version of image-based grouping. This latter component is similar to what is suggested from our data (Chapters 5 & 6). To test for higher-level modulations on rivalry, the distance between the rivalling elements could be manipulated. Since receptive field size tends to increase throughout the visual processing hierarchy, processing at a relatively late level allows for grouping at a larger inter-element spacing than early levels of processing. Previous studies on grouping during rivalry, including our own, have mainly used relatively short distances between elements. However, Blake and Alais (1999) found that grouping durations *decreased* with an increase in distance between the elements. In fact, a separation of 3 degrees between two 3-degree gratings was enough to abolish grouping. Such an experiment has, however, never been completed for images that rely on higher-level stages of the visual processing hierarchy, such as faces.

3 The lack of orientation tuning for flicker-and-swap rivalry

Although our results argue for an intricate role for image-content at a monocular level, flicker-and-swap rivalry did not appear to be affected by the relative image difference between the competing stimuli. In other words, we found no tuning for this form of rivalry. Note that this appears controversial since this form of rivalry is considered the hallmark of stimulus- (e.g. image-) rivalry. One explanation is that, under conditions of flicker-and-swap rivalry, competition bypasses the monocular channels where feature-

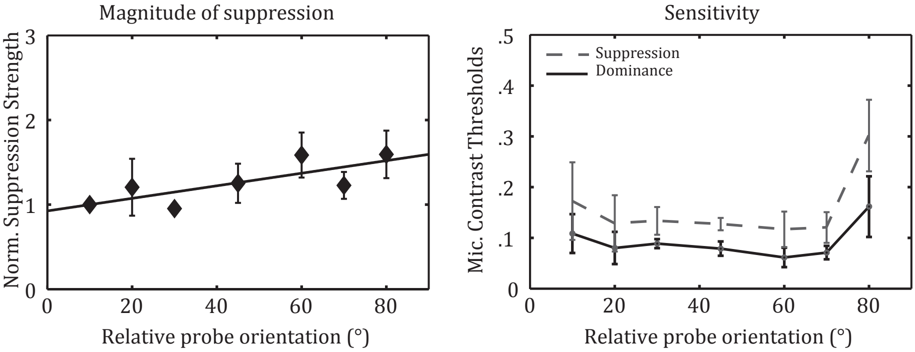


Figure 1:
Orientation tuning results using a flicker-and-swap paradigm from Chapter 2. The left panel shows the average strength of suppression for 4 observers. There is no tuning of the depth of suppression. The right panel shows contrast sensitivity thresholds during dominance and suppression. Sensitivity decreases when approaching the orientation of the suppressed image (0°) and the dominant image (90°) for during both dominance and suppression.

selective suppression arises (Wilson, 2003). Since orientation tuning is much broader and eventually even lost at later processing stages, no tuning should be evident in this 'higher-level' form of rivalry. However, this explanation may not be satisfactory since recent findings do demonstrate a monocular component to flicker-and-swap (Brascamp, Sohn, Lee & Blake, 2013).

Might tuning during flicker-and-swap rivalry simply have been overlooked because it was weak? A critical look at our data suggests that orientation tuning was not entirely absent: sensitivity during dominance was lowest for orientations most similar to the suppressed image (Figure 1). Since we found that sensitivity during dominance is also affected by the suppressed image in an orientation dependent manner (Chapter 3), a better comparison for our suppressed probe condition may have been a monocular version of our flicker-and-swap paradigm. In such an experiment, the suppressed grating would have been absent, leaving sensitivity during dominance unaffected to its orientation. Thus, to test whether suppression during flicker-and-swap rivalry shows a tuning profile similar to conventional rivalry, sensitivity to suppressed probes should be contrasted with sensitivity to the same probes presented in a monocular version of flicker-and-swap rivalry. In this monocular version, only one image will be swapped between the eyes, thus removing the effect of suppressed images unto dominant images.

Conclusion

In conclusion, the results presented in this thesis show strong interactions between aware and unaware visual information. These interactions are suggested to have an early, mainly monocular, locus. Likewise, the spatial dependencies seen for the outcome of rivalry competition (dominance) at multiple locations also appear to have a large early, monocular component. Moreover, our results suggest that higher-level modulation of dominance durations is rather weak. Taken together, the manipulations affecting perceptual suppression and dominance during binocular rivalry presented in this thesis will most likely affect processing at a monocular level of visual processing. In the context of the current dominant idea that rivalry is resolved at multiple stages of visual processing (Blake & Logothetis, 2002; Silver & Logothetis, 2007; Freeman, 2005; Lee, 2004; Nguyen, Freeman, & Alais, 2003; Wilson, 2003) our studies provide evidence that the early stages are strongly involved, while higher-level areas contribute only little to resolving binocular rivalry.

The transition from information contained in light to meaningful image representations involves many different stages of visual processing. As it turns out, early visual processing already appears to have a profound effect on determining what we will be aware of during binocular rivalry.

Chapter 8:

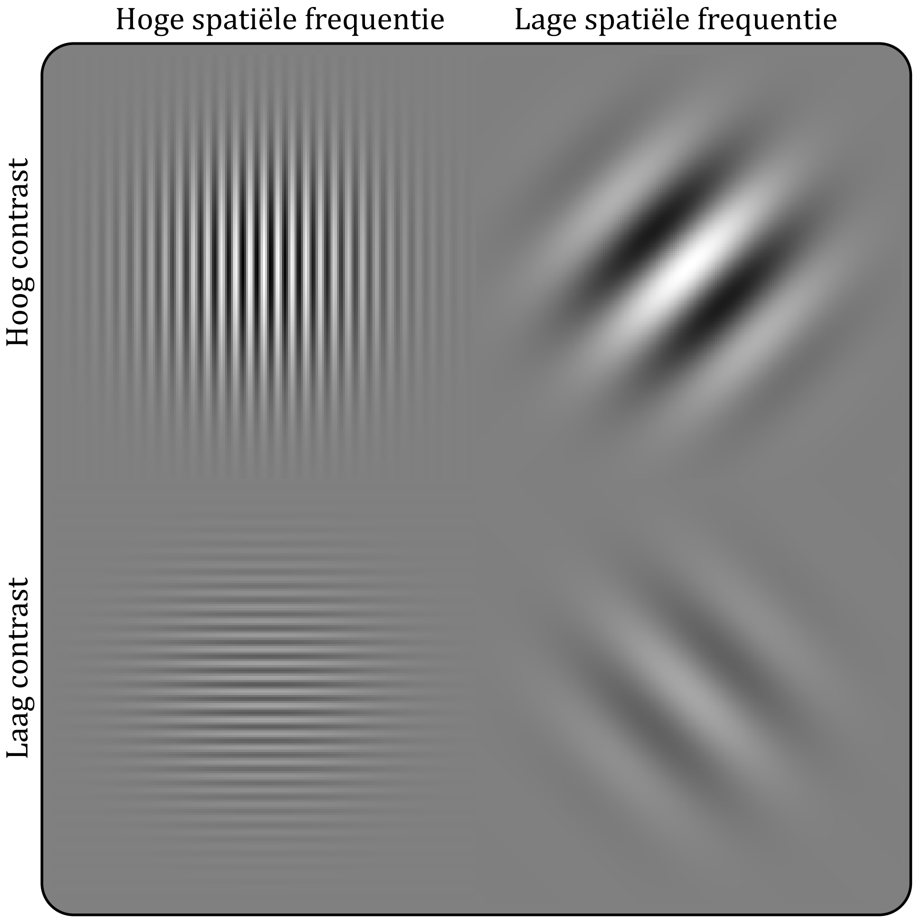
Nederlandse samenvatting

Bewuste en niet bewuste informatie

Zodra we wakker worden komt voor ons de wereld tot leven; we horen de vogeltjes fluiten en zien we de zonnestralen door de gordijnen. Onder de douche voelen we het warme water en daarna de zachte vezels van de handdoek. Even later kondigt de geur van versie koffie en een lekker stukje biefstuk met ei, een heerlijk ontbijtje aan. De dag begint met vele indrukken die ons aangeleverd worden door onze zintuigen. En natuurlijk zijn we ons graag bewust van deze zintuiglijke ervaringen, zeker wanneer we er van kunnen genieten. Toch, het is maar de vraag of we eigenlijk wel zo bewust zijn van al deze aangeleverde informatie. Momenteel denken wetenschappers juist dat veel van de sensorische informatie het niveau van het bewustzijn niet bereikt. In andere woorden, de informatie wordt wel, of in ieder geval deels verwerkt, maar we zijn ons daar niet altijd van bewust. Dit geldt voor alle zintuigen. Visuele waarneming, het onderwerp van deze dissertatie vormt hierop geen uitzondering.

Licht dat op het netvlies valt wordt via elektrochemische processen omgezet in verschillende typen stimulusinformatie. Denk daarbij onder andere aan helderheidcontrast, spatiële frequentie, oriëntatie, vorm en kleur (Figuur 1). Deze lokale bouwstenen van de waarneming worden steeds verder geïntegreerd door ons brein om uiteindelijk te resulteren in de complexe representaties van de wereld om ons heen. Deze cascade van processen kan beschreven worden aan de hand van een hiërarchie van visuele verwerkingsprocessen die steeds complexere en meer globale representaties vormen. Een van de vragen die waarnemingswetenschappers bezig houdt is op welk niveau van de visuele informatieverwerkingsproces de bewuste waarneming ontstaat.

Om deze vraag te beantwoorden is een specifieke visuele stimulus nodig die tot verschillen in bewuste ervaringen leidt. Met andere woorden, een constante stimulus die tot verschillende interpretaties kan leiden en waarvan er op elk moment maar één bewust is (en de andere interpretatie op dat moment dus onbewust blijft). Op deze manier is het mogelijk te onderzoeken wat het verschil maakt (bijvoorbeeld in breinactiviteit) tussen bewuste en onbewuste waarneming. Een bekend en goed onderzocht visueel fenomeen, dat bekend staat als binoculaire rivaliteit, maakt het mogelijk maakt om zo’n specifieke stimulus te creëren.



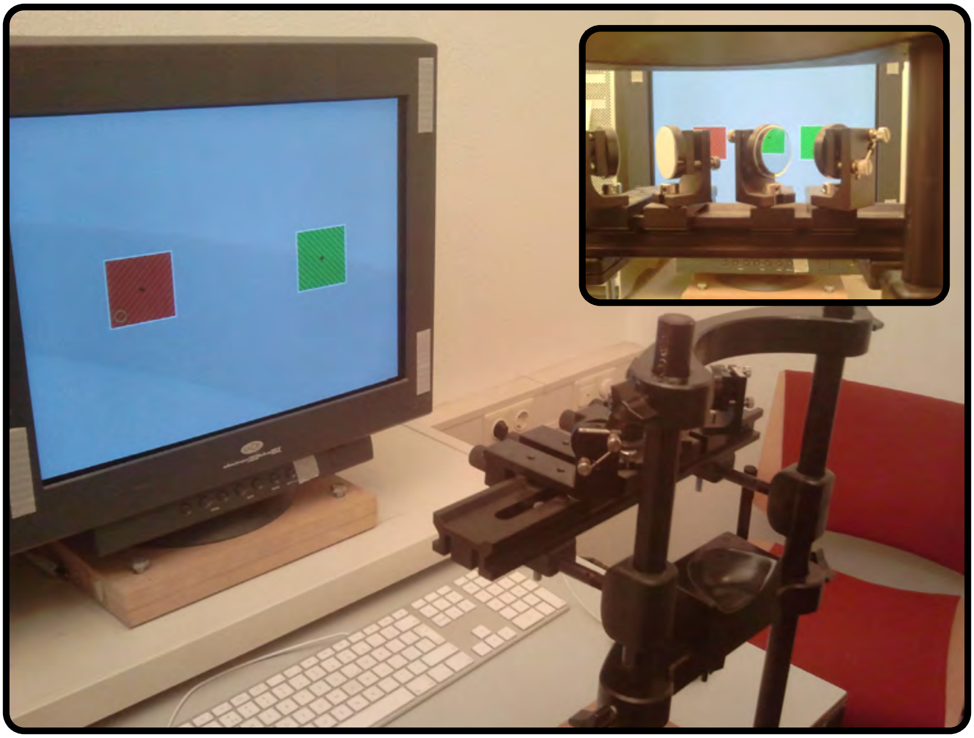
Figuur 1:
In dit figuur staan vier rasterpatronen met elk een andere stimulusinhoud: de informatie in de stimulus verschilt dus. De twee linker patronen hebben allebei een hoge spatiële frequentie. De twee rechter patronen hebben een lage spatiële frequentie. De spatiële frequentie is één van de lokale bouwstenen van de waarneming en beschrijft hoe vaak een helderheidovergang voorkomt binnen 1 graad van de visuele hoek (een deel van het oppervlak dat afhankelijk is van de kijkafstand). Bij een hoge spatiële frequentie komt zo'n helderheidovergang vaker voor.
Helderheidcontrast is een andere belangrijke bouwsteen. De twee bovenste patronen hebben een hoog helderheidcontrast: er is een groot verschil in de helderheid tussen de lichte en de donkere stukken van het patroon. Bij de onderste twee patronen is dat contrast een stuk lager. De helderheidverschillen zijn in deze patronen minder groot. Verder hebben alle patronen ook een andere oriëntatie van hun lijnen. De inhoud van deze stimuli kan heel specifiek gedefinieerd worden. Hierdoor worden dit soort stimuli vaak in het laboratorium gebruikt.

Binoculaire rivaliteit is een fenomeen dat optreedt wanneer de twee ogen verschillend gestimuleerd worden. Dat wil in de regel zeggen, als het ene oog een andere stimulus krijgt aangeboden dan het andere. In het lab wordt deze situatie gecreëerd met behulp van een zogenaamde spiegelstereoscoop (zie Figuur 2). Op die manier is het mogelijk om de twee verschillende stimuli zo aan te bieden dat ze op corresponderende gebieden op het netvlies van ieder oog vallen. Wanneer deze twee verschillende stimuli via de spiegelstereoscoop worden bekeken, zullen ze gaan *rivaliseren*. Dit betekent dat op ieder willekeurig moment slechts één van de stimuli bewust wordt waargenomen en dat met het verloop van de tijd de interpretaties worden afgewisseld. De stimulus die op een zeker moment bewust wordt waargenomen, wordt *perceptueel dominant* genoemd. De niet-waargenomen interpretatie wordt wetenschappelijk aangeduid met *perceptueel onderdrukt* (Figuur 3 illustreert hoe de lezer dit fenomeen zelf kan ervaren).

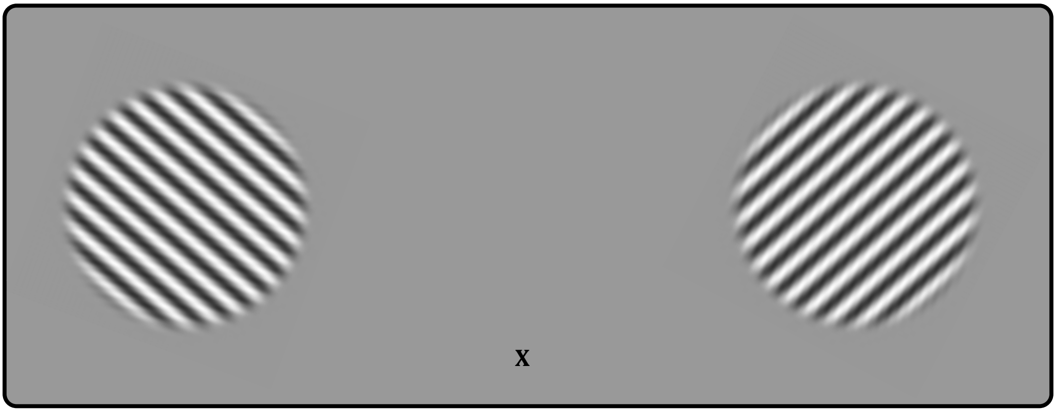
Binoculaire rivaliteit heeft het grote voordeel dat de visuele stimulus in de tijd constant blijft, terwijl de waarneming varieert, dat wil zeggen met het verloop van de tijd tussen de twee mogelijke interpretaties wisselt. We kunnen een proefpersoon vragen om zijn of haar waarneming te rapporteren wanneer we geïnteresseerd zijn in de dynamiek van deze wisselingen (denk aan duur en frequentie). Ook kunnen we dan kijken naar de invloed van de *niet* waargenomen op de *wel* waargenomen stimulus en visa versa, zolang we maar weten welke van de stimuli op een gegeven moment dominant is. Over wat die invloeden precies zijn, en hoe deze dominante en onderdrukte stimuli met elkaar interacteren, zijn de meningen tot op heden verdeeld.

Controverses rond onderdrukking

Dit proefschrift richt zich op twee controversiële ideeën over de invloed die waargenomen en niet-waargenomen stimuli op elkaar hebben tijdens binoculaire rivaliteit. De eerste controverse heeft betrekking op de aard van het proces dat tot onderdrukking tijdens rivaliteit leidt. Dit proces wordt ook wel *suppressie* genoemd. Sinds het klassieke paper door Blake en Fox in 1974 gaat men ervan uit dat niet-waargenomen stimuli in gelijke mate worden onderdrukt. Daarmee wordt bedoeld dat de inhoud van die stimulus, zoals bijvoorbeeld de verschillen in oriëntaties en de spatiële frequenties in de stimulus niet relevant is. Ongeacht de inhoud worden stimuli op dezelfde manier beïnvloed, wanneer de stimulus die via één oog binnenkomt, onderdrukt is. Een aantal onderzoekers heeft aangetoond dat dit niet het geval is: Niet alle stimuli worden *evenveel* onderdrukt. De mate van onderdrukking hangt volgens deze onderzoekers af van de informatie-inhoud



Figuur 2:
Foto van een spiegelopstelling met een stimulus voor binoculaire rivaliteit op het scherm. Deelnemers aan de experimenten plaatsen hun hoofd in de kinsteun. De spiegels veranderen de baan van de projectie die van de monitor komt. Hierdoor kunnen we de projecties van de twee stimuli op de monitor op corresponderende plaatsen van het netvlies laten vallen. Voor het visuele systeem staan er dan twee verschillende stimuli op dezelfde plek in de ruimte. Het gevolg is dat soms is het rode vierkantje bewust zichtbaar en dat wordt afgewisseld door het groene vierkantje. Deze wisselingen in de bewuste waarneming als gevolg van verschillende visuele input wordt binoculaire rivaliteit genoemd.



Figuur 3:
Dit is een voorbeeld van twee rasterpatronen die vaak gebruikt worden in rivaliteitexperimenten. Met een beetje moeite kan dit voorbeeld de lezer een indruk geven hoe rivaliteit, zoals in onze experimenten wordt ervaren: Houd figuur 3 op ongeveer 30 cm van u af en plaats uw wijsvinger op de x. Beweeg nu langzaam uw wijsvinger naar uw neus terwijl u op uw vinger blijft fixeren. Wanneer uw vinger ongeveer 10 cm van uw neus is en u de aandacht richt op de rasters in de achtergrond (waarbij u blijft fixeren op de vinger!) dan ziet u 3 rasterpatronen in plaats van twee. Richt uw aandacht nu op het middelste rasterpatroon maar blijf fixeren op uw vinger. De oriëntatie van het patroon - en dus uw bewuste waarneming - zal in de tijd veranderen. Dit fenomeen heet binoculaire rivaliteit.

van de twee stimuli (Abadi, 1976; O'Shea & Crassini, 1981). Ondanks deze vroege bevindingen, is dit bewijs voor een *selectief* proces tot recent overschaduwd door de grote hoeveelheid bewijs voor een *uniform* proces.

De tweede controverse heeft betrekking op de vraag op welk niveau in de visuele verwerkingshiërarchie de onderdrukking plaatsvindt. De resultaten van een groot aantal onderzoeken spreken elkaar tegen. Zo werd er aan de ene kant beargumenteerd dat rivaliteit op vroege verwerkingsniveaus moet plaatsvinden (o.a. Blake, 1989) terwijl anderen het standpunt verdedigden dat rivaliteit juist op een relatief laat verwerkingsniveau plaatsvindt (o.a. Logothetis et al., 1996). Als compromis tussen de twee (elkaar uitsluitende) standpunten wordt tegenwoordig over het algemeen een model gehanteerd, waarbij de rivaliteit tussen de twee stimulusrepresentaties op meerdere verwerkingsniveaus kan plaatsvinden (o.a. Blake & Logothetis, 2002). Dit standpunt voorziet echter ook in de mogelijkheid dat *elke* stap in de visuele verwerking belangrijk is voor perceptuele onderdrukking. Het is echter duidelijk dat perceptuele onderdrukking in belangrijke mate beïnvloedt wordt op in ieder geval twee verwerkingsniveaus: het *oogniveau* (ook wel aangeduid als het monoculaire niveau, dat voornamelijk een rol speelt in de eerste verwerkingstappen van het visuele systeem) en het *stimulusniveau* (dat voornamelijk een rol speelt in de latere verwerkingstappen van het visuele systeem). Met *oogniveau* wordt gerefereerd aan de bron van de visuele informatie: het oog waaraan een bepaalde stimulus wordt gepresenteerd. Met *stimulusniveau* gaat het om de informatie-inhoud van de rivaliserende stimulus, bijvoorbeeld de oriëntaties en spatiële frequenties (Figuur 1) in die stimulus. De relatieve bijdrage van deze twee invloeden, en wat de grootte van deze invloeden bepaalt, is nog niet bekend.

De hoofdstukken van dit proefschrift richten zich specifiek op de bovenstaande onbeantwoorde vragen. De eerste hoofdstukken richten zich op de interacties tussen de waargenomen en niet-waargenomen stimuli. Het gaat daar met name om de mate van onderdrukking en hoe deze afhangt van de informatie-inhoud van de twee stimuli. De laatste hoofdstukken richten zich voornamelijk op het kwantificeren van de invloed van de verschillende verwerkingsniveaus die een rol spelen tijdens rivaliteit. Dat wil zeggen, hoe groot de relatieve bijdragen van oog- en stimulusniveau zijn aan rivaliteit. Voordat we op dit laatste ingaan worden eerst de resultaten met betrekking tot al dan niet uniforme onderdrukking besproken.

Wat wordt er onderdrukt tijdens rivaliteit?

In Hoofdstuk 2 hebben we de controverse omtrent uniforme suppressie aangepakt door het fenomeen suppressie nader te belichten. We bepaalden hoeveel een patroon met een bepaalde oriëntatie onderdrukt wordt en hoe dat afhangt van de oriëntaties in de twee stimuli die met elkaar rivaliseren. Wij vonden, in tegenstelling tot het idee van uniforme suppressie, dat suppressie wel degelijk afhankelijk is van de informatie-inhoud van de rivaliserende stimuli. Met andere woorden, het maakt wel degelijk uit wat er aan de ogen wordt aangeboden. Dit lijkt weer vuur op de controverse te gooien, maar gelukkig werd ook duidelijk waarom eerdere studies dit resultaat niet vonden. In de proeven die *uniforme suppressie* aantoonden, voerden deelnemers vaak een taak uit op een target; een stukje visuele informatie dat werd toegevoegd aan een van de twee rivaliserende stimuli. De informatie had betrekking op de helderheid; de hoeveelheid licht dat op een oppervlak valt. Dit soort targets bevat echter weinig informatie die overeenkomt met de rivaliserende stimuli en is daarom niet voldoende aan de rivaliserende stimuli gerelateerd. Dat wil zeggen dat er een groot verschil is tussen de stimulusinhoud van de targets en die van de rivaliserende stimuli. Het relatieve verschil tussen deze targets en rivaliserende stimuli is dus erg groot. Onze resultaten tonen aan dat juist dat relatieve verschil tussen een target en de rivaliserende stimuli cruciaal is: een target dat lijkt op het onderdrukte stimulus wordt meer onderdrukt dan een target dat er niet op lijkt.

Er wordt vaak gezegd dat onderdrukking tijdens rivaliteit een wederkerig proces is: beide rivaliserende stimuli onderdrukken elkaar. De op een specifiek moment *sterkste* stimulus onderdrukt de andere stimulus het meest en is daarom dominant. Betekent dit dan dat een onderdrukte stimulus ook de waargenomen stimulus op een selectieve wijze beïnvloedt? De heersende opvatting is dat de dominante waarneming tijdens rivaliteit niet verschilt van de situatie waarin slechts een enkele stimulus wordt aangeboden aan een van beide ogen (Tsuchiya, Koch, Gilroy & Blake, 2006; Alais & Blake, 2005). Met andere woorden, de idee is dat de onderdrukte stimulus geen invloed heeft op hetgeen dat op dat moment wordt waargenomen.

Onze resultaten over selectieve onderdrukking suggereren echter dat de onderdrukte stimulus wel degelijk invloed kan uitoefenen. Het effect van suppressie lijkt immers wederkerig tijdens rivaliteit. De dominante stimulus zou dus ook op een selectieve manier kunnen worden beïnvloed door de onderdrukte stimulus. In Hoofdstuk 3 hebben we een vergelijkbare methode als in Hoofdstuk 2 gebruikt, met dit verschil dat onze interesse nu uit ging naar wat er gebeurt met de dominante stimulus. We onderzochten hoe targets die in de waargenomen stimulus worden gepresenteerd, worden beïnvloed door wat er aan het andere oog wordt gepresenteerd. We vergeleken ook de bewuste waarneming van de targets in de dominante stimulus tijdens rivaliteit met de waarneming van dezelfde targets in dezelfde stimulus maar dan zonder dat er een rivaliserende stimulus aan het andere oog werd aangeboden. Zoals voorspeld, toonden onze resultaten aan dat de aanwezigheid van een onderdrukte stimulus wel degelijk effect heeft op de dominante waarneming. Verder laten onze resultaten zien dat de inhoud van de onderdrukte stimulus beïnvloedt hoe een dominante stimulus wordt waargenomen. Deze invloed is dus wederkerig: In Hoofdstuk 2 lieten we al zien dat hetgeen wij niet waarnemen ook wordt beïnvloed door wat dat we wel waarnemen. Kortom, de mate van onderdrukking hangt af van het verschil in de stimulusinhoud van de rivaliserende stimuli. Deze conclusie geldt echter voor de situatie als twee stimuli op één plek met elkaar rivaliseren: de interactie tussen twee *geïsoleerde* stimuli. Rivaliteit kan echter plaatsvinden op meerdere locaties tegelijk. Is de onderdrukking op elke plek in het visuele veld gelijk? Met andere woorden, is onderdrukking tussen rivaliserende stimuli uniform over verschillende locaties? In Hoofdstuk 4 onderzochten we deze vragen. We gebruikten twee stimuli die opgebouwd waren uit heel veel kleinere, losstaande elementen, die allemaal individueel rivaliseerden. Een van deze twee stimuli had echter een afwijkend element. Uit ons eerder onderzoek (zie Hoofdstuk 2) weten we dat lokale interacties tussen de waargenomen en de niet-waargenomen stimulus cruciaal zijn voor de mate van onderdrukking. Om de lokale interacties gelijk te houden waren de lokale verschillen in onze stimulus hetzelfde over het gehele rivaliserende veld. Dit werd gerealiseerd door het verschil in oriëntatie tussen ieder corresponderend element (dus inclusief het afwijkende) in beide stimuli gelijk te houden. Om uniforme onderdrukking over het visuele veld te onderzoeken maakten we de stimulus met het afwijkende element onzichtbaar. Vervolgens gaf de proefpersoon aan wanneer en waar de onderdrukte stimulus zichtbaar werd. Bij uniforme onderdrukking was de verwachting dat het afwijkende element geen invloed zou hebben op het moment en de plek van zichtbaar worden, bij niet-uniforme onderdrukking zou het afwijkende element als eerste zichtbaar moeten worden. De resultaten toonden aan dat ook hier de onderdrukking niet uniform was. De afwijkende elementen kwamen als eerste uit de fase van onderdrukking, Dat wil zeggen ze werden als eerste zichtbaar als de dominante stimulus werd afgewisseld. De mate waarin iets opvalt bleek hierin een cruciale rol te spelen. We vonden een relatie tussen de opvallendheid wanneer het element bewust wordt waargenomen en de mate waarin datzelfde element onderdrukt wordt. Dit laat zien dat hoe opvallend iets is zelfs een rol speelt buiten de bewuste waarneming.

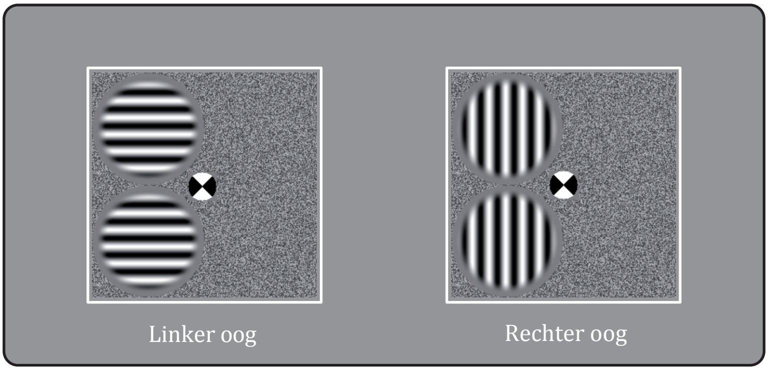
Het kwantificeren van de oog- en stimulusinvloeden op binoculaire rivaliteit

Tot zo ver hebben we ons gericht op de invloed van *onderdrukte stimuli* op de waargenomen stimuli en andersom. Omdat de mate van onderdrukking verschilt per locatie, onderzochten we ook hoe een perceptueel dominante stimulus op *één* locatie de waarneming van een rivaliserende stimulus op een *andere* locatie kan beïnvloeden. Dit experiment was gericht op het onderzoeken van de relatieve bijdragen van twee veronderstelde verwerkingsstadia die betrokken zijn bij binoculaire rivaliteit (de 2^e controverse): de invloed van het specifieke oog en de invloed van de specifieke stimulus. Om deze invloeden, die ook ten grondslag zouden liggen aan de hierboven beschreven interacties tussen waargenomen en niet-waargenomen stimuli, te onderscheiden ontwikkelden we nieuw paradigma. Hiermee kunnen we kwantificeren hoe groot de invloed van de bron van de stimulus (het specifieke oog waaraan het gepresenteerd wordt) is op wat er op een bepaalde locatie wordt waargenomen, en ook hoe groot de invloed van de specifieke stimulusinhoud hierop is. Dit paradigma is gebaseerd op eerder onderzoek waaruit bleek dat twee aangrenzende rivaliserende elementen die dezelfde oriëntaties bevatten langer tegelijk waargenomen worden dan wanneer deze elementen verschillende oriëntaties bevatten (Alais & Blake, 1998). Dit effect werd toegeschreven aan visuele verwerking op een niveau waar de bron van de informatie (het oog, of een monoculair kanaal) geen rol meer speelt, kortom waar de invloed van de specifieke stimulus bepalend is en niet die van het oog (Kovács, Papathomas, Yang, and Fehér, 1996).

In Hoofdstuk 5 onderzochten we de invloed van oog- en stimulus inhoud op de tijdsduur dat twee rivaliserende elementen tegelijk zichtbaar zijn. Hiervoor presenteerden we twee losstaande elementen op twee locaties aan één oog en twee andere elementen op dezelfde locaties aan het andere oog. Voor beide locaties gold dat aan één oog een element met een horizontale oriëntatie werd gepresenteerd en aan het andere oog een element dat een verticale oriëntatie bevatte. Met andere woorden, er werd een situatie gecreëerd waar er op meerdere plekken in het visuele veld tegelijk rivaliteit optrad. Verder konden de elementen die aan één oog gepresenteerd werden dezelfde of verschillende oriëntaties bevatten (zie Figuur 4). Omdat de elementen in deze stimulus los van elkaar kunnen rivaliseren waren er voor de proefpersonen op elk moment verschillende combinaties van waargenomen elementen mogelijk. Afhankelijk van wat de proefpersoon waarnam, en hoe de stimulus was opgebouwd, bepaalden we in hoeverre oog- en stimulusinformatie de bewuste waarneming beïnvloeden. Als een stimulusconfiguratie zoals in figuur 4B (met dezelfde oriëntatie op verschillende locaties in verschillende ogen) werd aangeboden, leidde tot het tegelijk waarnemen van twee elementen met dezelfde oriëntatie, kan verondersteld worden dat alleen de *stimulus*inhoud de tijdsduur van een dergelijke waarneming bepaalde. Wanneer deze stimulusconfiguratie leidde tot het tegelijk waarnemen van twee elementen met verschillende oriëntaties, veronderstellen we deze tijdsduur bepaald werd door juist alleen het *oog* van aanbieding.

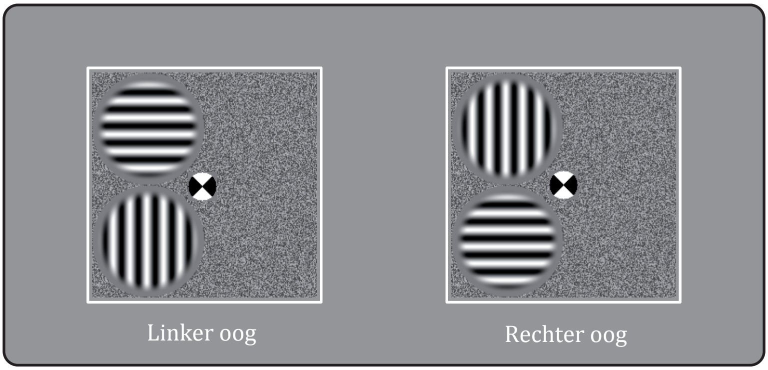
A)

Zelfde oriëntaties aan elk oog gepresenteerd



B)

Verschillende oriëntaties aan elk oog gepresenteerd



Figuur 4:
In Hoofdstuk 5 presenteerden we twee losstaande elementen op twee locaties aan één oog. Aan het andere oog presenteerde we twee andere elementen op dezelfde locaties. Voor beide locaties gold dat aan één oog een element met een horizontale oriëntatie werd gepresenteerd en aan het andere oog een element dat een verticale oriëntatie bevatte. Hierdoor werd een situatie gecreëerd waar er op meerder plekken in het visuele veld tegelijk rivaliteit optrad. Verder konden de elementen die aan één oog gepresenteerd werden dezelfde of verschillende oriëntaties bevatten. Wij onderzochten hoelang de verschillende combinaties van waargenomen element zichtbaar bleven. Hiermee konden we bepalen in hoeverre oog- en stimulusinformatie de bewuste waarneming beïnvloeden.

De resultaten waren als volgt: Voor stimuli die horizontale of verticale oriëntaties bevatten, bleek stimulusinhoud inderdaad van belang te zijn. Toch was de invloed van stimulusinhoud relatief klein in vergelijking met de invloed van de bron van de twee elementen: het oog waar de informatie vandaan kwam. Wat opviel was dat wanneer de stimuli diagonale oriëntaties bevatten, de rol van stimulusinvloed compleet wegviel: twee elementen die dezelfde diagonale oriëntatie bevatten bleken alleen langer samen bewust te worden waargenomen wanneer zij aan hetzelfde oog werden gepresenteerd. De bron van de elementen (dus het oog waaraan ze aangeboden worden) speelt daarmee een cruciale rol in de bepaling van de tijdsduur dat elementen samen bewust worden waargenomen. Op basis van deze resultaten zou de conclusie kunnen zijn dat stimulusinhoud van ondergeschikt belang is bij het groeperen van rivaliserende stimuli. Echter, uit de resultaten van Hoofdstuk 2 blijkt dat stimulusinhoud wel degelijk van invloed kan zijn op rivaliteit: lokale onderdrukking wordt sterk beïnvloed door de informatie-inhoud van de rivaliserende stimuli. Het is mogelijk dat bovenstaande experimenten de globale invloed van stimulusinhoud onderschatten, omdat de stimuliverschillen enkel op één soort stimuluskenmerk (namelijk oriëntatie) betrekking hebben. Van oriëntatie is algemeen bekend dat de verwerking al vroeg plaatsvindt. Zo vroeg zelfs, dat informatie over de bron van de stimulus verstrengeld is met de informatie-inhoud van de stimuli: dezelfde hersencellen die in mindere of meerdere mate selectief zijn voor specifieke oriëntaties in de stimulus, zijn dit ook voor de bron van de informatie (het oog waar de informatie vandaan komt). Om stimulusinvloed beter te kunnen bepalen is een stimulus nodig waarvan de inhoud door het brein verwerkt wordt, onafhankelijk van oog waaraan de stimulus wordt aangeboden.

Om er achter te komen of stimulusinhoud voornamelijk van invloed is op dit latere verwerkingsniveau is in Hoofdstuk 6 bovenstaand paradigma uitgebreid. We gebruikten in het nieuwe experiment stimuli waarvan de inhoud pas selectief wordt verwerkt in hersengebieden die niet differentiëren tussen de twee mogelijke bronnen (het oog waaraan het was aangeboden). Hiervoor gebruikten we gezichten. Van deze stimuli is bekend dat ze relatief laat in het visuele systeem selectief worden verwerkt. Omdat gezichten ook nog eens als een geheel worden verwerkt, is de verwachting dat hierbij de invloed van stimulusinhoud een stuk groter zal zijn. Uit de resultaten bleek dit niet het geval te zijn. De tijdsduur dat twee elementen die met elkaar één gezicht vormden samen waargenomen werden was niet anders dan voor twee abstracte stimuli als rasters die dezelfde oriëntatie bevatten en ook samen werden waargenomen. De conclusie is dan ook dat alleen de visuele verwerking die vroeg in de verwerkingshiërarchie plaatsvindt, bepalend is voor de tijdsduur dat twee elementen samen bewust worden waargenomen. De invloed van de relatief late verwerking op de vroege visuele verwerking is dus gering.

Conclusie

We weten dat niet alle sensorische informatie tot bewuste waarneming leidt. Dit geldt ook voor de visuele waarneming. Toch hebben bewust en niet bewust waargenomen stimuli een sterke invloed op elkaar. In dit proefschrift is duidelijk gemaakt dat de bewuste waarneming wordt beïnvloed door wat wij niet waarnemen, maar ook dat wat wij *niet* waarnemen wordt beïnvloed door wat we *wel* waarnemen. Ook is duidelijk geworden dat de waarneming op één locatie in het visuele veld sterk afhankelijk is van de waarneming op een andere locatie. De processen die hieraan ten grondslag liggen lijken al op een vroeg verwerkingsniveau binnen het visuele systeem plaats te vinden. Onze resultaten passen daarom niet goed bij het huidige, algemeen geaccepteerde, compromis aangaande rivaliteit, dat stelt dat de competitie op meerdere verwerkingsniveaus plaatsvindt. Onze resultaten suggereren juist dat deze veronderstelde verwerkingsniveaus samen plaatsvinden in de vroege verwerkingsniveaus van het visuele systeem. Dit betekent dat zelfs de eerste stappen in de visuele verwerking al een belangrijke rol spelen in de vorming van de bewuste waarneming.

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Curriculum vitae

Sjoerd Martin Stuit was born in Waalwijk, the Netherlands on Oktober 29, 1981. He initially went to the Johannes Calvijn highschool in Rotterdam. In 1995 he changed schools and graduated at the Albeda College in Rotterdam in 2001. After a two years of full time employment at various jobs he decided to go back to school. In 2003 he enrolled in Maatschappelijk Werk en Dienstverlening at the HRO in Rotterdam. After an inspirational course in Psychology, Sjoerd switched to the Univeristy of Utrecht in 2004. There he completed his Bachelors in Psychology in 2007 and continued his studies by enrolling in the research master program Cognitive Neuroscience. During this two-year research master he spent six month in Prof. Dr. David Alais' lab at Sydney University. Immediately after graduating in 2009 he started as a PhD-student supervised by Prof. Dr. Frans Verstraten and Dr. Chris Paffen. In 2010 Dr. Maarten van Der Smagt joined the team. In 2013, Sjoerd spent three month at Vanderbilt University to work with Prof. Dr. Randolph Blake. Before returning to academia, Sjoerd aims to finish the restoration of his car.