THE ANALYSIS OF CONTINUOUS FLASH SUPPRESSSION

By

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Dissertation

Submitted to the Faculty of the

Graduate School of Vanderbilt University

in partial fulfillment of the requirements

for the degree of

DOCTOR OF PHILOSOPHY

In

Psychology

December, 2011

Nashville, Tennessee

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ACKNOWLEDGEMENTS

I am truly grateful to my advisor, Randolph Blake, for taking a chance with me as his graduate student. I could not have asked for a better academic advisor and mentor in life. I am also grateful to the other members of my Dissertation Committee, Isabel Gauthier, Jeffrey Schall, and Alan Freeman, and my Qualifying Committee, David Zald, Geoffrey Woodman, and Ronald Cowan, for providing me with invaluable input and great discussions. I also thank my lab members/ participants, Sam Ling, Jan Brascamp, Min-Suk Kang, Sammy Hong, and David Bloom, for helping me through my graduate career. Finally I would like to thank my friends and family for all their support. My research would not have been possible without the financial support of the Vanderbilt Vision Research Center.

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CHAPTER I

INTRODUCTION

We are continuously exposed to more sensory information than we can possibly attend to and process in detail. Since it is not always obvious which information is most relevant, in many instances it would be adaptive for neural processes to continue monitoring sensory signals that fall outside of awareness. In turn, those signals may play a significant role in shaping our perceptual experiences and guiding our behavior without our knowledge. Several lines of research suggest that unperceived visual information may indeed influence perceptual and cognitive operations (e.g. reviews by Bridgeman, 1992; Goodale, 2004; Merikle, 1998). While evidence in support of 'unconscious' visual processing may seem intriguing, it is not always compelling that stimuli are in fact presented outside of observers' awareness in these studies (e.g. Kouider & Dehaene, 2007; Merikle, 1992). Luckily, psychophysical techniques in rendering stimuli perceptually invisible have progressed and now include motion induced blindness, attentional blink, and crowding, among others (review by Kim & Blake, 2005). What is so compelling about these and other approaches is that the perceptual 'suppression' of a stimulus seems practically indistinguishable from the physical removal or absence of that stimulus. One kind of technique exploits the natural suppression that occurs when different images are simultaneously presented to the two eyes (Figure 1.1). An advantage of dichoptic stimulation techniques over other approaches is that experimenters can present a variety of salient stimuli over extended periods of time and continue to observe reliable suppression. Binocular rivalry (Breese, 1909; Wheatstone, 1838), flash suppression (Wilke, Leopold, & Logothetis, 2003; Wolfe, 1984), flicker-swap rivalry (Logothetis, Leopold, & Scheinberg, 1996) and binocular switch suppression (Arnold, Law, & Wallis, 2008), are among a few of the techniques that induce such potent perceptual suppression.

Recently, one particular interocular suppression technique has become increasingly popular as a means for “erasing” visual stimuli from awareness. Coined ‘continuous flash suppression’ (or CFS) by Tsuchiya and Koch (2005), this style of binocular rivalry involves rapidly flashing contour-rich noise patterns to one eye in order to perceptually suppress the stimulus presented to the other eye. Suppression with CFS is so potent that observers solely perceive the dynamic CFS display (while the stimulus in the opposing eye is rendered perceptually invisible) for extended periods of time, which are reportedly 10 fold longer than suppression produced with traditional binocular rivalry (Tsuchiya & Koch, 2005). The experimentally controlled onset and duration of invisibility with CFS also deviate from the unpredictable fluctuation in perception typically observed with conventional binocular rivalry. In comparison to CFS, temporally sensitive techniques such as masking and attentional blink paradigms are constrained by short stimulus durations (Kim & Blake, 2005). In addition, perceptual suppression with CFS is less susceptible to the effects of unstable fixation and eye movements in comparison to suppression induced by crowding and motion induced blindness paradigms (Kim & Blake, 2005). Thus, CFS offers several methodological advantages over other psychophysical techniques and viewed in this light, it is not surprising that researchers have become fond of utilizing CFS in order to investigate stimulus processing outside of awareness. The following section reviews those findings.

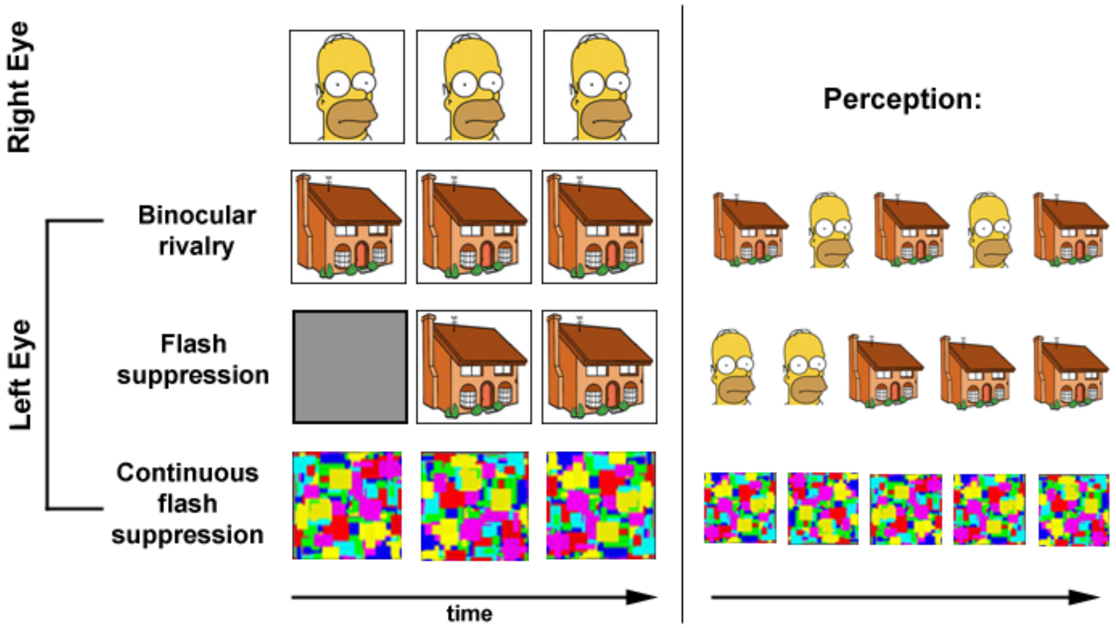

Figure 1.1: Illustrations of 3 interocular suppression techniques. During binocular rivalry, dissimilar stimuli are presented dichoptically for a continuous period of time. As a result, perception unpredictably fluctuates between the two images. Initially during flash suppression, a stimulus is solely presented to one eye. That stimulus is perceptually suppressed once another stimulus is abruptly flashed into the other eye. During continuous flash suppression, a dynamic sequence of images is presented to one eye and the image presented to the other eye is suppressed for an extended period of time.

Behavioral and physiological findings with CFS

Several CFS studies have utilized a well-established psychophysical paradigm in which prolonged neural adaptation to a stimulus gives rise to visual aftereffects. These adaptation aftereffects have been used for several decades to isolate and probe the neural mechanisms selective for different stimulus attributes, ranging from low-level properties such as spatial frequency and orientation to high-level features such as face identity and expression (Mollon, 1974; Thompson & Burr, 2009). One way to investigate the extent of stimulus encoding under interocular suppression is to determine whether full-blown adaptation occurs when the inducing stimulus is suppressed from awareness during the adaptation period. If full-strength adaptation aftereffects can be induced despite interocular suppression, it would imply that the neural events responsible for adaptation are unaffected by suppression and transpire regardless of observers' awareness of the inducing stimulus. On the other hand, adaptation may be disrupted by suppression, resulting in aftereffects that are weakened or even abolished (Blake, Tadin, Sobel, Raissian, & Chong, 2006; Wiesenfelder & Blake, 1990). When this strategy is applied using CFS to suppress an adapting stimulus, experiments show that CFS effectively weakens neural adaptation, leading to reduced aftereffects specific to a number of properties of the suppressed stimulus, including spatial phase (Tsuchiya & Koch, 2005), orientation (Kanai, Tsuchiya, & Verstraten, 2006), motion (Maruya, Watanabe, & Watanabe, 2008) and contrast (Shin, Stolte, & Chong, 2009; E. Yang, Hong, & Blake, 2010). Furthermore, aftereffects thought to be driven by 'high-level' adaptation are abolished, which includes complex motion aftereffects (Maruya et al., 2008) and several face adaptation aftereffects (Amihai, Deouell, & Bentin, 2010; Moradi, Koch, & Shimojo, 2005; Shin et al., 2009; Stein & Sterzer, 2011).

In summary, the suppressive effects of CFS undoubtedly hinder the analysis of diverse stimulus attributes. If suppression greatly influences the encoding of these fundamental visual properties, one could reasonably assume that it would similarly affect any combination of these features, underlying the neural representations of more complex image properties. However, other lines of research suggest that certain classes of complex stimuli continue to be processed despite being blocked from visual awareness by CFS.

For instance, there is an emerging consensus that some neural processes involved in face perception remain operational when images of faces are suppressed from awareness using CFS. Evidence supporting this conclusion comes from experiments using a technique that measures the amount of time that an initially suppressed stimulus remains suppressed, the assumption being that select stimuli should emerge from suppression sooner if aspects of those stimuli continue to be processed during suppression. This technique is based on a hallmark characteristic of binocular rivalry: stronger stimuli remain suppressed for shorter periods of time (Levelt, 1965). Using this technique, Jiang, Costello, and He (2007) presented face stimuli to observers' suppressed eye and measured the time it took for faces to emerge from suppression and become visible. Upright faces gained dominance faster than inverted faces (see also Stein, Hebart, & Sterzer, 2011a; E. Yang, Zald, & Blake, 2007) and this inversion effect under suppression appears specific to the category of faces, in comparison to house stimuli (G.M. Zhou, Zhang, Liu, Yang, & Qu, 2010). The face inversion effect was used as evidence that face-selective mechanisms were operational during the unconscious presentation of upright faces. However, there is growing speculation as to whether upright and inverted faces are processed differently (e.g. Loftus, Obert & Dillon, 2004; Richler, Mack, Palmeri, & Gauthier, 2011; Sekuler, Gaspar, Gold, & Bennett, 2004) and so the face inversion effect may not be an informative measure in dissociating object-specific processes. Even so, physiological data also suggests that faces, or rather the configuration of face features, are weakly encoded under CFS. Residual neural activity in response to faces suppressed with CFS has been consistently reported using a variety of physiological techniques, including functional magnetic resonance imaging or fMRI (Jiang & He, 2006; Sterzer, Haynes, & Rees, 2008), electroencephalography or EEG (Jiang et al., 2009) and magnetoencephalography (Sterzer, Jalkanen, & Rees, 2009). This line of research has now inspired investigators to examine whether social cues in faces, such as gaze direction, can also be unconsciously processed (Stein, Senju, Peelen, & Sterzer, 2011b).

There is further evidence, obtained using the “time to break suppression” strategy (Jiang et al., 2007), to suggest that the emotional overtones expressed in faces are encoded under CFS. For instance, when faces with different facial expressions were presented under CFS, faces portraying fearful expressions emerged from suppression faster than those with neutral or happy expressions (Sterzer, Hilgenfeldt, Frequdenberg, Bermpohl, & Adli, 2011; Tsuchiya, Moradi, Felsen, Yamazaki, & Adolphs, 2009; E. Yang et al., 2007). Studies measuring face adaptation aftereffects demonstrated that, unlike other face attributes (e.g.

identity, gender, shape), aftereffects specific to facial expressions could still be induced, albeit more weakly, when the inducing face stimulus was suppressed from awareness (Adams, Gray, Garner, & Graf, 2010; E. Yang et al., 2010). Furthermore, neuroimaging and EEG studies have reported robust neural activity in response to suppressed (fearful) facial expressions, particularly in the face-responsive areas of the superior temporal sulcus and the amygdala (Jiang & He, 2006; Jiang et al., 2009), which are also areas associated with affective processing. Altogether these findings support the emerging claim that affectively-laden stimuli are preferentially processed in the absence of observers' awareness and attention of those stimuli (e.g. LeDoux, 1996; Vuilleumier, Armony, Driver, & Dolan, 2001; but see Pessoa & Ungerleider, 2003). Furthermore, among those who hold this view, many speculate that this process occurs through subcortical projections that bypass early visual cortical areas to support the rapid emotional evaluation of sensory signals (e.g. LeDoux, 1996; Morris, Ohman, & Dolan, 1998; Vuilleumier, Armony, Driver, & Dolan, 2003).

Behavioral and physiological effects have been reported with other categories of meaningful objects besides faces that are rendered invisible owing to CFS. In particular, there are some who believe that areas in the dorsal visual pathway that are involved in visually guided actions are also responsible for registering images of highly-manipulable of objects (e.g. Chao & Martin, 2000; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995). According to lesion studies, the encoding of such objects in the dorsal pathway furthermore may not depend on observers' perception of those objects (reviews by Goodale & Milner, 1992;

Stoerig & Cowey, 1997). Almeida, Mahon, Nakayama, and Caramazza (2008) presented images of objects in different categories (i.e. animals, tools, vehicles) as prime and target stimuli and the former was suppressed with CFS. Observers' performance in categorizing targets was facilitated when the target was preceded by an invisible prime of the same object category. Interestingly this category-related priming effect occurred only for the tool category, suggesting that this object category may be preferentially processed under suppression. Consistent with this, Fang and He (2005) reported robust blood oxygen level dependent (BOLD) activity in object-sensitive dorsal regions that were selective for tool images regardless of whether they were visible or invisible consequent to CFS; object-sensitive ventral areas showed very weak responses to suppressed images, relative to when those images were not suppressed (but see Hesselmann & Malach, in press). Fang and He (2005) speculated that visual signals of tool images may have been accessed by the dorsal pathway through subcortical projections that bypass V1 or, alternatively, through the magnocellular pathway which, they believe, is more resistant to interocular suppression (He, Carlson, & Chen, 2005; Lin & He, 2009).

Researchers have also found that linguistic meaning could be extracted from stimuli suppressed from visibility by CFS. For instance, images of morphemes that are part of one's native language tend to emerge from suppression faster than images of unfamiliar, foreign words (Jiang et al., 2007). Similarly, a word tends to emerge faster from suppression induced by CFS when that word is preceded by a semantically related visible word (Costello, Jiang, Baartman, McGlennen, & He, 2009; but see Kang, Blake, & Woodman, in press). On the other hand, words with a negative-connotation may be suppressed for longer periods of time under CFS than words with neutral affect (Y.H. Yang & Yeh, 2010). Categorical and numerical priming effects have also been observed with invisible prime stimuli portraying names of tools and numbers, respectively (Almeida, Mahon, & Caramazza, 2010; Almeida et al., 2008; Bahrami et al., 2010). Overall, evidence implies that with CFS, semantic information of an invisible stimulus may be encoded and, consequently, may strengthen the neural signals associated with that stimulus such that it emerges more quickly from suppression.

While it may seem intuitive that attentional resources can only be allocated to stimuli that we perceive (Block, 1996), studies using CFS suggest that this intuition is incorrect. Attention can, in fact, be involuntarily drawn to the location of a stimulus suppressed by CFS, particularly if that stimulus is emotionally arousing (Jiang, Costello, Fang, Huang, & He, 2006). Other CFS studies report that spatial attention (Shin et al., 2009; E. Yang et al., 2010) or feature-based attention (Kanai et al., 2006) directed towards a suppressed adapting stimulus can enhance the potency of that stimulus so that it induces a stronger visual aftereffect. Likewise, when attentional resources are fully removed from a suppressed stimulus, resulting adaptation aftereffects are substantially weakened (Bahrami, Carmel, Walsh, Rees, & Lavie, 2008) and related neural responses are reduced in magnitude as well (Bahrami, Lavie, & Rees, 2007). Therefore, attention may modulate the strength or level of processing performed under suppression, successfully boosting or weakening neural signals arising from the suppressed stimulus.

Caveats of findings with CFS

Studies using CFS are used as evidence for the functional significance of processing certain stimulus properties without awareness. While this interpretation seems intriguing, evidence is not entirely unequivocal. In several studies, behavioral effects were exclusively measured under conditions of CFS and so it is unclear to what extent these effects occur when observers are *aware* of the stimuli and whether these effects with CFS are relatively substantial in magnitude (e.g. Almeida et al., 2008 & 2010; Bahrami et al., 2007 & 2008). In other studies, the behavioral effects observed with CFS were not replicated under visible conditions and so it is unclear as to the purpose of these effects when they only occur without awareness (e.g. Costello et al., 2009; Jiang et al., 2006 & 2007; Stein et al., 2011b; Y.H. Yang & Yeh, 2010; G.M. Zhou et al., 2010). Take for example, studies that measure the ”time to break suppression” of images such as faces. In a separate ‘control’ experiment, faces and CFS stimuli were binocularly presented and the contrast of the face was gradually increased during a trial in order to mimic the perceptual experience of the face’s emergence from suppression. The face inversion effect has not been reliably found in control experiments (Jiang et al., 2007; Stein et al., 2011a; G.M. Zhou et al., 2010). If face inversion effects are only observed when faces are invisible and the effect is considered evidence of face processing, it seems unreasonable to infer that face processing does not occur with visible faces. Rather, the absence of an inversion effect with visible faces tends to be used as supporting evidence that any reaction time (RT) differences across CFS conditions are not attributed to differences in response criteria, detection ability, or low-level visual properties, since the same differences are not observed under visible conditions.

In CFS studies, conclusions about the measured effects purportedly surviving suppression rest critically on the ability of observers to reliably judge the extent to which the critical stimulus is indeed completely suppressed from awareness (see Kang et al., in press). Investigators using CFS typically create their own measure of awareness that is implemented as a separate ‘control’ experiment. In some studies, observers have been instructed to discriminate between a stimulus used in the experimental condition and a grid-scrambled version of that (or another) stimulus while both are being presented under CFS (Almeida et al., 2008; Fang & He, 2005; Jiang et al., 2006 & 2009; Jiang & He, 2006). Still in other studies, observers were instructed to categorize the suppressed stimulus into one of two object categories (e.g. tool versus animal or human versus non-human; Almeida et al., 2008 & 2010; Arnold et al., 2008; Bahrami et al., 2008; Sterzer et al., 2008 & 2009). If performance was at chance in discriminating between different types of suppressed stimuli, investigators concluded that observers were unaware of the stimuli presented under CFS. However, the inability to recognize a stimulus should not be confused with the inability to detect the presence of a stimulus under suppression. Such discrimination measures cannot rule out the possibility that some visual features of a suppressed stimulus can be detected by the observer, with this residual information actually driving the effect observed under CFS. Indeed, there is evidence that different aspects of a stimulus suppressed by CFS can be in different states of suppression (Hong and Blake, 2009).

Other investigators collected observers' subjective reports of perception during experimental trials (using key presses) in order to correlate observers' awareness with the measurement of interest (Adams et al., 2010; Bahrami et al., 2010; Tsuchiya and Koch, 2005) or to reliably initiate probes under perceptual suppression (Maruya et al., 2008; Tsuchiya, Koch, Gilroy, & Blake, 2006). However, subjective measures of awareness are susceptible to response bias and demand characteristics (Lin & He, 2009), and no CFS study to date has attempted to objectively measure detection performance, using signal detection theory for example. Notably, Sterzer and colleagues (2009) monitored observers' perception of suppressed stimuli during experimental trials using both a detection and discrimination task and found that observers' level of awareness did not differ across performance on each task.

When looking at findings from CFS studies alone, the evidence for visual processing outside of awareness seems very compelling. It is important to note, however, that the stimulus conditions creating CFS constitute a form of binocular rivalry, i.e., dissimilar monocular stimuli presented to corresponding areas of the two eyes. And we know there exists a wealth of evidence on visual processing during rivalry suppression, and some of that evidence differs substantially from what is found using CFS. Since the magnitude of suppression under CFS is reportedly 3 fold greater than suppression induced with binocular rivalry (Tsuchiya et al., 2006), it is reasonable to assume that visual signals are more strongly attenuated with CFS. Why, then, do some aspects of visual information processing seemingly survive CFS when other studies imply that those aspects of processing are abolished during suppression phases of rivalry? For instance, with CFS affective and semantic components of stimuli can influence the duration that those stimuli remain suppressed, typically facilitating their emergence from suppression (e.g. Costello et al., 2009; Jiang et al., 2007; Mudrik, Breska, Lamy, & Deouell, 2011; E. Yang et al., 2007; Y.H. Yang & Yeh, 2010;). Although studies have demonstrated that emotional overtones can modulate a stimulus' predominance in BR (e.g. Alpers & Gerdes, 2007; Bannerman, Milders, De Gelder, & Sahraie, 2008; Coren & Russell, 1992; Ogawa & Suzuki, 2000), none have reported that the suppression durations of such a stimulus are specifically affected. Blake (1988) found no evidence that presenting words or meaningful text under BR suppression would break suppression faster than nonsense strings of letters (see also Zimba & Blake, 1983). Overall there is weak evidence to suggest that semantic information can shorten BR suppression but rather, these forms of contextual cues are known to lengthen stimulus dominance during BR and more likely reflect the top-down influence of attention on rivalry dynamics (review by Blake & Logothetis, 2002).

Similarly, attention and priming effects observed with CFS have not been reported with BR. Schall, Nawrot, Blake, and Yu (1993) did not find evidence that visual cues could direct spatial attention under rivalry suppression, unlike Jiang and colleagues (2006) who reported positive effects using CFS. Similarly, object priming effects observed with stimuli suppressed with CFS (Almeida et al., 2008) are not found when stimuli are suppressed during BR (Cave, Blake, & McNamara, 1998).

Neuroimaging findings show that neural responses to suppressed stimuli are weakened both by CFS and by BR suppression (reviews by Lin & He, 2009; Tong, Meng, & Blake, 2006). However, residual activity in high-level visual areas is reported more frequently with CFS (Fang & He, 2005; Hesselmann & Malach, in press; Jiang & He, 2006; Jiang et al., 2009; Sterzer et al., 2008) than with rivalry suppression (Pasley, Mayes, & Schultz, 2004; Williams, Morris, McGlone, Abbott, & Mattingley, 2004). In one of the first studies to examine BOLD activity during BR, Tong, Nakayama, Vaughan, and Kanwisher (1998) showed that category-specific responses (i.e. in fusiform face area and parahippocampal place area) were abolished when corresponding stimuli (i.e. images of faces or houses) were suppressed during rivalry. On the other hand, a recent study showed that responses in these same object-specific areas could be reliably extracted when related stimuli were presented under CFS (Sterzer et al., 2008). Thus in contrast to CFS, there is little evidence for high-level computations under standard BR suppression which, ironically, is reputed to be the weaker form of interocular suppression. While methodological differences between CFS and BR studies could partly contribute to the discrepancy among findings, the point is that CFS findings of high-level unconscious processing is not as compelling when examined within the context of all BR research.

Research Purpose and Objectives

Visual processing involves a series of neural operations that are carried out in hierarchical stages along parallel pathways (e.g. Livingstone and Hubel, 1988; Schmolesky et al., 1998; Van Essen, Anderson, & Felleman, 1992). Early mechanisms operate locally within small regions of the visual field, encoding image properties in terms of their spatial and temporal features. Such features refer to contour "size" (defined in terms of spatial frequency) and orientation as well as the changes in the distribution of those features over time within a given region of the visual field. At later stages in the visual hierarchy, those local feature representations are combined to register more complex image properties (e.g. 3D shape, texture, global motion), eventually leading to the neural representation of objects and events.

The emerging picture from studies using CFS is that visual processing of certain categories of stimuli can occur even when those stimuli are presented outside of awareness. The operation of detectors tuned to the physical properties (e.g. contrast, orientation, motion) of the suppressed stimuli seem to be effectively attenuated by CFS (e.g. Kanai et al., 2006; Maruya, et al., 2008; Tsuchiya & Koch, 2005). Despite weakened input from early neural mechanisms, advanced stages of analysis may continue to operate, resulting in observable effects thought to be driven by meaningful properties of the invisible stimulus, such as object category and stimulus valence (review by Lin & He, 2009). Thus it is unclear at what stage(s) of visual processing CFS imposes its influence on neural representations of stimuli. If all visual signals to the suppressed eye are effectively abolished by CFS, the neural events that give rise to suppression would have to occur at a relatively early stage of analysis; only when suppression fails (meaning the observer is aware of the stimulus) would visual signals be encoded. On the other hand if the signal fidelity is fully preserved under CFS, suppression would transpire in subsequent stages of analysis after the neural representation of that stimulus has been formed. However, the current body of evidence is seemingly at odds with both of these interpretations.

Recently, Lin and He (2009) proposed an alternative framework for understanding the level of visual processing under interocular suppression. Some invisible local features can be registered and combined to create a neural representation of that stimulus, given the availability of attentional resources. However, the fidelity of that representation may depend on the class of visual input (e.g. object category) and thus the underlying neural events specific to the processing of that stimulus class. This could imply that CFS operates selectively within different neural areas where those categories of objects or object properties are represented. For instance, suppression may be strongest within functionally specialized areas that reside along the ventral visual pathway, which are thought to correlate strongly with perception (Rees, Kreiman & Koch, 2002). In contrast, areas that are unperturbed by CFS may be those that reside along the dorsal visual pathway as well as the subcortical pathway presumably responsible for the registration of affective-content (e.g. Jiang & He, 2006; Lin and He, 2009). Such an interpretation has huge implications concerning the type of information and, importantly, the functional significance of information that can influence perception and behavior outside of awareness and attention.

Before accepting that framework, however, scientific convention dictates that we are obliged to consider simpler, more parsimonious explanations. This dissertation focuses on the possibility that CFS may operate exclusively at a relatively early stage in visual processing, where it differentially impacts the local features that define various classes of objects. Such selectivity could be the result of the spatio-temporal nature of CFS itself, for example. Stimulus features that are weakly suppressed may be effectively processed, but not necessarily without awareness since features that are weakly suppressed are more likely to be visible to observers. Regardless of observers' awareness, this would imply that stimulus-driven effects that survive CFS are primarily an artifact, or side effect, of the visual nature of the CFS stimulus, rather than the consequence of meaningful attributes of the suppressed stimulus itself. Thus, interpreting the residual effectiveness of certain stimulus classes under CFS requires that we first understand what CFS is actually suppressing. Only then can we determine at what stage suppression is occurring and identify the nature of the information processed without awareness. In other words, we need to understand the nature of this inferential tool – CFS – before we can interpret the consequences of using it in studies of visual processing.

The objective of this study is to investigate the visual properties that empower CFS by sampling select regions of the multi-dimensional feature space within which CFS might produce potent suppression. In particular, I explored the local spatio-temporal feature space associated with the CFS stimulus that is most frequently utilized to date; I examined how certain properties of CFS influenced observers' sensitivity to information viewed by the suppressed eye. The aim of Experiment 2.1 and Experiment 2.2 was to obtain evidence that the currently popular CFS stimulus is indeed biased at suppressing certain stimulus features. The aim of Experiment 3.1 and Experiment 3.2 was to further attribute this bias to the visual properties of the CFS stimulus and to their interaction with the properties of the suppressed stimulus. Specifically, I measured the selectivity and magnitude of suppression for the spatial frequency and orientation properties of the suppressed stimulus and examined whether these measures vary as function of the spatial frequency and temporal frequency content of the CFS display. The magnitude of suppression is used to gauge the degree to which neural signals are attenuated by CFS. This can be indexed by comparing detection thresholds to a stimulus when it is perceptually suppressed and when it is visible. The selective nature of suppression, to the extent that it exists, should be reflected in the differences among measured threshold elevation levels as stimulus features are varied under CFS. Only by first learning answers to these questions can we draw conclusions about the nature of the stimulus representation being suppressed by CFS, the extent to which a stimulus is processed without awareness, and the neural substrates of suppression induced by CFS.

CHAPTER II

MODULATION OF SUPPRESSION BY THE SPATIAL FEATURES OF THE SUPPRESSED STIMULUS

CFS refers to a potent form of interocular suppression wherein a visual stimulus presented to one eye is suppressed from awareness as a result of a rapidly displayed series of randomly generated patterns high in contrast and rich in contours that is presented to the other eye (in this dissertation I will refer to this potent suppressing stimulus as the CFS display). CFS was first created using a montage of different sized rectangles whose luminance and locations varied randomly over time, with each montage resembling a Mondrian-like pattern. Tsuchiya and Koch (2005), the inventors of this display, did not tell us why this particular stimulus design was chosen, but for the last few years it has been the most frequently utilized CFS display (e.g. Amihai et al., 2010; Hesselmann & Malach, in press; Hong & Blake, 2009; Kanai et al., 2006; Mudrik et al., 2011; Yamada & Kawabe, in press; E. Yang et al., 2007 & 2010; Y.H. Yang & Yeh, 2010; W. Zhou, Jiang, He, & Chen, 2010). Some laboratories have created their own versions of CFS display that still satisfy the general characteristics of the original version (i.e. rapidly flashing, contour rich patterns) and that also effectively suppress visual awareness of a rival stimulus viewed by the other eye (e.g. Adams et al., 2010; Almeida et al., 2008 & 2010; Bahrami et al., 2007 & 2008; Costello et al., 2009; Maruya et al., 2008; Sterzer et al., 2008 & 2009).

In general, the physical properties of CFS displays seem to be somewhat random in nature. Given that suppressed stimuli are typically not equated or controlled for in terms of low level properties (with the exception of contrast in some cases), this leaves the impression that suppression must be non-selective in nature. That is, a stimulus is strongly suppressed irrespective of its spatio-temporal properties, the properties of the suppressor and the difference in properties of the two rival stimuli. There is good reason to believe that this could be the case. Several binocular rivalry studies indeed show that observers' sensitivity to probe features such as luminance, chromaticity, spatial frequency, and orientation are all significantly attenuated when probes are presented during suppression phases of rivalry (Blake & Fox, 1974; Nguyen, Freeman & Wenderoth, 2001). Furthermore, probe suppression does not seem to depend on differences in the physical properties between the rival stimuli themselves, including differences in grating orientation (Blake & Lema, 1978), luminance (Hollins & Bailey, 1981; Makous & Sanders, 1978), contrast (Blake & Camisa, 1979), spatial frequency (Holopigian, 1989) and stimulus complexity (Freeman & Li, 2009). This consistent pattern of findings have led to the notion that binocular rivalry suppression is nonselective, meaning that visual responses to all kinds of probes are adversely affected when presented under suppression.

However, there is growing evidence that there may be another component of rivalry suppression that is selectively tuned to the properties of the stimulus being suppressed (Alais & Melcher, 2007; Alais & Parker, 2006; Apthorp, Wenderoth, & Alais, 2009; Li, Freeman, & Alais, 2005; Ling & Blake, 2010; Ooi &

Loop, 1994; E.L. Smith, Levi, Harwerth, & White, 1982; Watanabe, Paik, & Blake, 2004; Westendorf, 1989). For instance, Stuit, Cass, Paffen, and Alais (2009) showed that impairment in contrast sensitivity was strongest for probes that were similar to the suppressed stimulus in terms of orientation or spatial frequency content; suppression depth declined as the probe deviated along those feature dimensions. Furthermore, Ling & Blake (2010) showed that the orientation tuning-bandwidth was also broadened, suggesting increased noise in the signal representation of the suppressed stimulus (also Sengpiel, Blakemore, & Harrad, 1995a). These findings imply that, not only is the neural representation of a stimulus weakened, but it may also be significantly altered under suppression. What do we know about the characteristics of suppression produced by CFS?

In the original study that introduced CFS, Tsuchiya and Koch (2005) reported that negative afterimages were weakened when the inducing stimulus – a Gabor patch -- was perceptually suppressed, with longer periods of suppression yielding greater reductions in afterimage strength. In their preliminary experiments, investigators found that they could influence the amount of time that the Gabor patch was visible by manipulating the spatial frequency of that stimulus. Specifically, complete suppression occurred less frequently with Gabor patches of high spatial frequency (2 cycles per degree or cpd) in comparison to Gabor patches of low spatial frequency (0.6 cpd; Figure 2.1). This finding suggests that CFS may differentially affect the suppressed eye's stimulus depending on the spatial frequency content of that stimulus. We cannot be certain about this however, because Tsuchiya and Koch tested only 2 spatial frequencies and did not adjust the contrast of their Gabor patches to accommodate differences in baseline contrast sensitivity at different spatial frequencies.

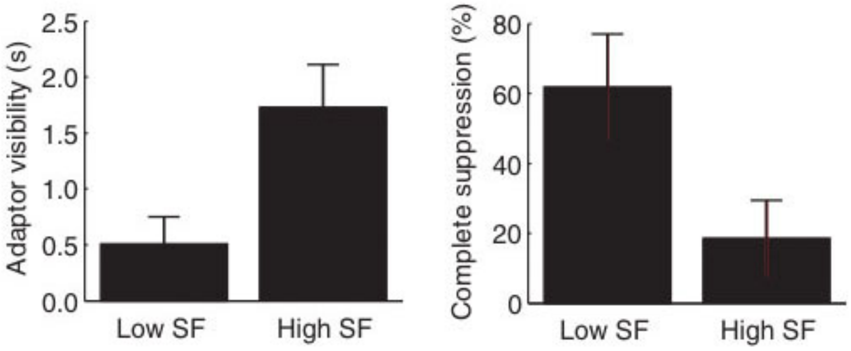

Figure 2.1: Results of Tsuchiya & Koch (2005). Observers tracked visibility of an inducing stimulus during periods of adaptation. Plotted are mean duration of visibility (left) and proportion of trials of complete suppression (right) for the inducing stimulus as a function of its spatial frequency.

The experiments of Chapter II investigated systematically the effects of CFS on observers’ contrast sensitivity measured over a wide range of spatial frequencies and orientations for stimuli presented to the suppressed eye. A forced-choice technique was used to estimate contrast thresholds for detecting target stimuli presented to one eye when that eye was suppressed by a CFS display presented to the other eye (CFS condition) and when it was not suppressed (baseline condition). If CFS does indeed exert differential effects on processing of stimuli with different spatial features, detection thresholds in the CFS condition should vary depending on the spatial features of the suppressed stimulus. But if CFS operates uniformly on all spatial features, elevations in detection thresholds should be comparable in magnitude relative to baseline measures. The CFS display used throughout this dissertation consisted of Mondrian-like patterns very similar to those used in most other published CFS studies.

Experiment 2.1: Spatial frequency of the suppressed stimulus

General Method

Participants

Six observers including the investigator participated in each experiment. Observers were recruited from the Vanderbilt University Psychology Department and local Nashville area and several were experienced psychophysical observers. All had normal or corrected-to-normal acuity and good stereopsis. With the exception of the investigator, participants were naïve to the purpose of the study and provided written consent prior to participation.

Apparatus

Stimuli were presented on the left and right halves of a gamma-corrected CRT monitor (21” Sony Multiscan; 1024 x 768 resolution; 100 Hz refresh rate) and were viewed at a distance of 92 cm in a darkened room. Stimuli were generated on a G4 Power Macintosh computer running MATLAB supplemented by the Psychophysics toolbox (Brainard, 1997; Pelli, 1997). All experiments employed 10-bit luminance resolution using bit stealing. Stimuli were viewed through a mirror stereoscope with mounted chin- and head-rests, which presented the stimulus in the right half of the display exclusively to the right eye and the stimulus in the left half of the display exclusively to the left eye.

Procedure

Prior to each main experiment, the root mean square (RMS) contrast of the CFS images was determined individually for each observer in order to avoid ceiling or floor effects when measuring contrast thresholds under CFS. That is, if the contrast of the CFS display is set too high, observers' will fail to detect the target stimulus in the suppressed eye even when the target stimulus is presented at full contrast. The contrast of the CFS display was set to a value sufficient to produce significant elevations in contrast thresholds relative to baseline while at the same time being weak enough so that observers were able to detect the target stimulus at relatively high contrast values. Moreover, the optimal CFS contrast can vary substantially across observers since individuals vary widely in terms of the depth of suppression (e.g. Norman, Norman, & Bilotta, 2000). CFS contrast was determined based on observers' performance on a short task immediately prior to the first CFS session. The task and stimuli were identical to the main experiments with the exception that, instead of the target stimulus contrast varying across trials, the target stimulus was fixed at a high contrast (e.g. 75% Michelson contrast in Experiment 3.1) and the CFS display varied across trials at intervals of 5% or 10% RMS contrast. The maximum CFS contrast at which the target stimulus was detectable more than 90% of the time was the contrast used for the main experiments.

Method

Stimuli

The target stimulus was a Gabor patch of 1° radius (sinusoidal grating enveloped by a circular Gaussian) presented at one of six spatial frequencies: 0.5, 1, 2, 4, 8 or 12 cpd. The Gabor patch was oriented either 10° clockwise or counter-clockwise of vertical and the orientation and phase (180° reversal) were randomly chosen for each trial. The Gabor patch was embedded in 1D broadband Gaussian noise (2° x 2°, 10% RMS contrast) to prevent baseline thresholds from reaching the floor and to increase task difficulty.

The CFS display consisted of a dynamic series of achromatic Mondrian-like patterned images made of rectangles drawn in variable size (0.12° - 0.59° in length), luminance, and location within a 2° square aperture of uniform mean luminance (15 cd/m^2). Prior to each trial, Mondrian images were generated and normalized for contrast and mean luminance, which was determined individually for each observer (see General Methods). The Mondrian images changed every 100 ms (10 Hz) throughout a trial. Binocular fusion contours surrounding the stimuli and fixation dots were present at all times to promote stable binocular eye alignment. Stimuli were presented against a uniform gray background at mean luminance (15 cd/m^2).

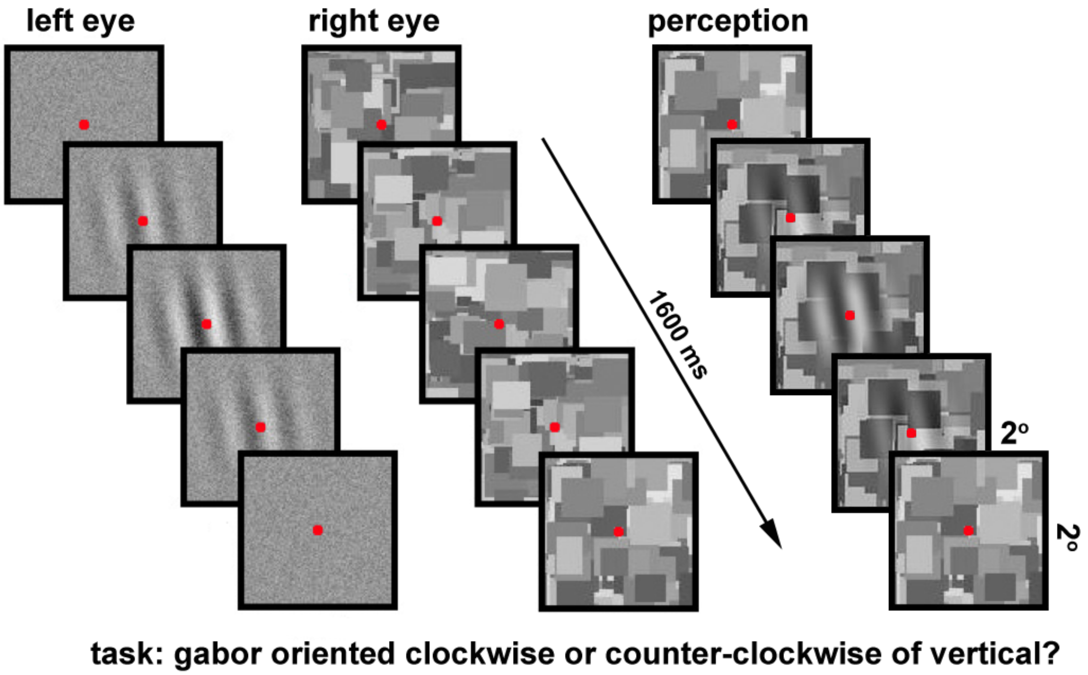

Figure 2.2: Illustration of a trial sequence including CFS in Experiment 2.1.

Procedure

On each trial, a Gabor stimulus of a given spatial frequency was presented to one eye while the opposing eye viewed at the corresponding retinal position a dynamic CFS display (10 Hz) or a blank field at mean luminance. The eye that received the Gabor stimulus varied across trials and is described later. The contrast of the Gabor stimulus linearly increased from 0 during the initial 300 ms in order to avoid abrupt transients. For 1 s, the Gabor stimulus remained at a set contrast predetermined by the QUEST adaptive staircase procedure (Watson & Pelli, 1983). In the remaining 300 ms, the Gabor stimulus decreased in contrast in order to reduce subsequent negative afterimages. A trial lasted 1.6 seconds, during or after which observers made their response for a 2 alternative-forced-choice (2AFC) orientation discrimination task, indicating whether the

Gabor was oriented clockwise or counter-clockwise of vertical. No feedback was given and the subsequent trial began 600 ms after a response was made (Figure 2.2).

Observers participated in 4 sessions, 2 devoted to the measurement of contrast detection thresholds when the Gabor was suppressed with CFS and 2 devoted to baseline threshold measurements when CFS was absent. The first two sessions always involved CFS. All 6 spatial frequency conditions were presented within a session. To prevent trials of one spatial frequency from influencing visibility of trials of other spatial frequencies (Hubner, 1996), the conditions were blocked within a session and the order of conditions was randomized across sessions.

The QUEST adaptive staircase procedure produced estimates of contrast thresholds at 75% performance for Gabor patches at 6 different spatial frequencies. Four thresholds were obtained for each spatial frequency condition and for both session types (CFS and baseline). A session consisted of 2 randomly interleaved staircases per condition: each staircase measured the contrast threshold for the Gabor viewed by a given eye (i.e. 1 staircase for the left eye and the other staircase for the right eye). Each staircase consisted of 50 trials and with 12 staircases in each session (4), observers performed 600 trials per session and a total of 2,400 trials for the experiment. Practice trials were performed prior to the first session. Each session took approximately 30 minutes to complete.

Results & Discussion

Mean contrast sensitivity was expressed as the reciprocal of the mean threshold contrast estimated from the staircase procedure. A 2 x 6 (session type x Gabor spatial frequency) repeated measures ANOVA on mean contrast sensitivity values resulted in a main effect of CFS ($F(1,5)=70.2$, $p<.001$, effect size: $\eta_p^2=0.9$) and Gabor spatial frequency ($F(5,25)=49.6$, $p<.001$, $\eta_p^2=0.9$). Mean contrast sensitivity was significantly lower in the CFS sessions (mean ± standard error of the mean or SEM= 9.2 ± 0.7) in comparison to baseline sessions (23.1 ± 1.4), which indicates that CFS was effective at suppressing the Gabor stimulus. Mean contrast sensitivity exhibited an inverted U shape function with Gabor spatial frequency (0.5 cpd= 4.5 ± .4; 1 cpd= 9.9 ± 1.1; 2 cpd=19.1 ± 1.2; 4 cpd= 24.0 ± 1.4; 8 cpd= 24.3 ± 1.6; 12 cpd= 15.1 ± 1.5), consistent with the normal human contrast sensitivity function (e.g. Robson, 1966). Figure 2.3 illustrates contrast sensitivity functions for each observer across sessions.

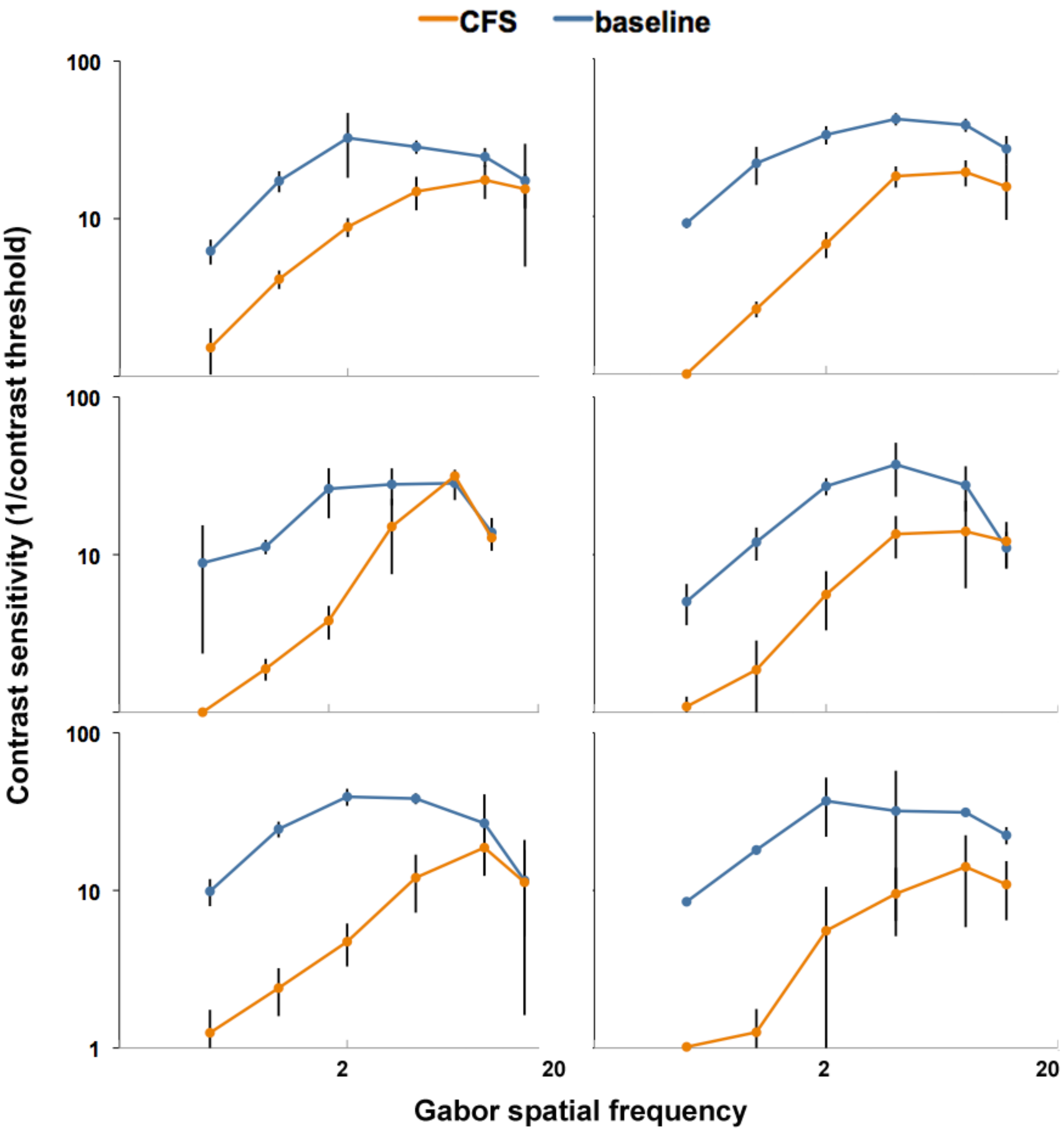

Figure 2.3: Individual results of Experiment 2.1. Each plot represents the contrast sensitivity functions obtained for each observer during CFS (blue) and baseline (orange) sessions. Axes are in log scale and error bars denote standard deviation.

Most importantly there was a significant interaction between session type and Gabor spatial frequency (F(5,25)=24.6, *p*<.001, η_p^2=0.8). Mean contrast sensitivity was significantly attenuated by CFS for all spatial frequencies (*p*<.001 to *p*=0.03) with the exception of the highest spatial frequency (12 cpd, *p*=0.1). To compare detection threshold estimates for various Gabor spatial frequencies and to account for the natural asymmetries in the human contrast sensitivity function, a threshold elevation index was computed as the log ratio of the mean threshold estimate for detecting a grating of a given spatial frequency under CFS to the mean baseline threshold estimate for detecting that same grating without CFS (Figure 2.4). When comparing threshold elevation values across conditions of increasing spatial frequency, suppression depth was significantly greater for the 1 cpd condition relative to the 2 cpd condition (t(5)= 2.6, *p*=.05) and the 2 cpd relative to the 4 cpd condition (t(5)=5.8, *p*=.002).

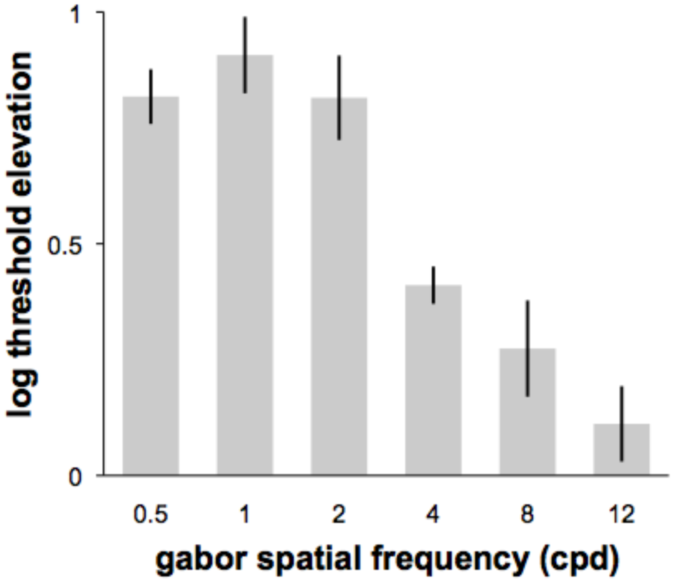

Figure 2.4. Group results of Experiment 2.1. Plotted is the elevation in contrast thresholds for detecting a Gabor patch of a given spatial frequency when it was suppressed with CFS, relative to baseline thresholds. Error bars denote standard error of the mean (SEM).

Results from Experiment 2.1 show that suppression produced by CFS differentially impairs sensitivity dependent on the spatial frequency content of the stimulus viewed by the other eye. Contrast thresholds under CFS were strongly elevated when the suppressed eye viewed a Gabor patch of low spatial frequency (0.5-2 cpd) and threshold elevations weakened as the stimulus further increased in spatial frequency. To determine whether these findings can be generalized to other, more complex stimuli, an additional experiment was performed in which contrast thresholds were measured for detecting the location of bandpass filtered face images suppressed with CFS (Appendix A). Consistent with results of Experiment 2.1, contrast thresholds were more strongly elevated with low bandpass filtered faces (centered on 0.75 cpd) than with high bandpass filtered faces (centered on 6 cpd, Appendix A, Figure A.2). These results extend the initial findings by Tsuchiya and Koch (2005) suggesting that CFS attenuates low spatial frequency information more than it attenuates high spatial frequency information. The results from Experiment 2.1 are further discussed later in this chapter, in conjunction with findings from the next experiment.

Experiment 2.2: Orientation components of the suppressed stimulus

Method

Stimuli

The suppressed stimulus was an achromatic noise pattern (4° x 4°; 10% RMS contrast) randomly generated prior to each trial in which each pixel was assigned a luminance value taken from a uniformly random distribution of values between 0 and 1. The noise pattern was then bandpass filtered in the orientation domain (20° bandwidth), with orientation frequencies centered either at 0°, 45°, 90° or 315° (where 0° denotes vertical). The noise pattern was also spatial frequency bandpass filtered (<19 cpd) to minimize artifacts that occur when approaching the Nyquist frequency (~20 cpd). Filtering was performed in the Fourier domain using a 2D Finite Impulse Response filter and smoothed to reduce aliasing. The probe was a contrast increment (3.3° x 2°) that occurred above or below fixation. The probe emerged gradually following a Gaussian contrast ramp (100 ms) to avoid abrupt onset transients. Contrast along the probe edges were also spatially smoothed using a Gaussian filter to reduce the perception of edges produced by large differences in contrast.

The CFS displays (4° x 4°; 10 Hz) were generated in a manner identical to those implemented in the previous experiment. The CFS display consisted of gray-scale Mondrian-like patterns that were normalized in mean luminance (15 cd/m^2) and RMS contrast, which was determined individually for each observer (see General Methods). Five hundred CFS images were pre-drawn prior to each block of trials and stored in video memory.

A mask image (4° x 4°) was presented at the end of each trial and was randomly composed of black and white (93.6 cd/m^2) pixels. Binocular fusion contours surrounding the stimuli and fixation dots were presented at all times to promote stable binocular eye alignment. Stimuli were presented against a homogenous field at mean luminance (15 cd/m^2).

Procedure

At the beginning of a trial, an orientation bandpass filtered noise stimulus was presented to an observer's dominant eye. The non-dominant eye simultaneously received either a dynamic CFS display or a gray field (baseline) in the corresponding retinal location, depending on the session. After 500 ms, the probe gradually emerged on the upper or lower half of the noise stimulus and remained present for 500 ms. The peak contrast of the probe was determined using a staircase procedure. The target and CFS displays were removed from the screen 1 s after trial onset. A mask stimulus was presented dioptically in the same location in order to reduce possible negative afterimages. The mask also signaled the observer that a response should be made by pressing one of two buttons to indicate the location (top or bottom half) of the probe stimulus. Feedback was given following each response, and the subsequent trial began after 200 ms (Figure 2.5).

The experiment consisted of 2 sessions. The first session collected baseline threshold measurements of the target display when it was presented without CFS and allowed observers' to become acclimated to the task and probe stimuli. The second session measured contrast thresholds for probe detection when the stimulus was paired dichoptically with the CFS display. Within a session, each of the 4 conditions (probe orientation) was presented in separate blocks of trials and the condition order was randomized across sessions. Each block involving CFS began with 3 'example' trials in which the pedestal stimulus was presented without CFS (identical to the baseline condition). These example trials were to inform observers of the probe orientation that they were to detect. Four randomly interleaved 2 down/1 up staircases were executed in each block and each terminated after 12 reversals. Similar to the procedure used by Tsuchiya et al. (2006), the contrast step size was reduced by half after every four reversals and began at 30% of the initial contrast increment/decrement. Contrast detection thresholds representing 71% correct performance (Levitt, 1971) were estimated from the mean of the probe contrast values of the last 8 reversals. When an individual's estimated thresholds did not properly converge, additional thresholds were collected. Practice trials were performed prior to each session and the experiment took approximately 1.5 hours to complete.

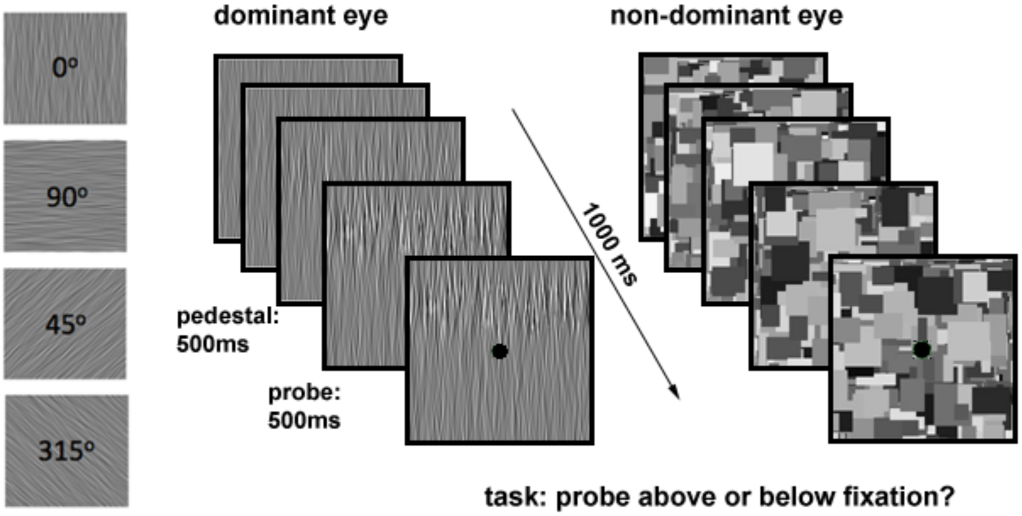

Figure 2.5: Illustration of a trial sequence including CFS in Experiment 2.2. The suppressed stimulus was an orientation bandpass filtered display that was centered on one of four orientations (left).

Results & Discussion

Contrast thresholds were entered into a 2 (session) x 2 (orientation category: cardinal vs. oblique) x 2 (orientation angle) repeated measures ANOVA. There was a main effect of session ($F(1,5)=18.1$, $p=.008$, $\eta_p^2=0.8$) in which thresholds were significantly elevated in the CFS session (0.26 ± 0.04) relative to the baseline session (0.14 ± 0.01). The main effect of orientation was close to significant (F(1,5)= 4.8, *p*=.079, η_p^2=0.5); probe thresholds for the two cardinal orientations (0.21 ± 0.02) were higher than those for the two oblique orientations (0.19 ± 0.02). There was neither a main effect of orientation angle nor any interaction with orientation angle and cardinal conditions were later averaged as well as oblique conditions. Importantly, the interaction between session and orientation category was significant (F(1,5)=8.6, *p*=.03, η_p^2=0.6).

To examine this interaction a threshold elevation index for each orientation condition was calculated as the log ratio of the mean threshold estimate obtained under CFS to the mean baseline estimate obtained without CFS. As shown in Figure 2.6, CFS produced a greater relative threshold elevation for detecting cardinal orientations (group: 0.33 ± 0.03) in comparison to detecting oblique orientations (group: 0.2 ± 0.06, t(6)=3.3, *p*=0.02). There were large individual differences, which may be attributed to differences in the general strength of interocular suppression: observers who showed large differences between the cardinal and oblique conditions exhibited overall weaker suppression than the remaining observers. It is also possible that individual differences may have been partly attributed to astigmatisms, which observers were not tested for. However, the trend in results was consistent for 5 out of the 6 observers.

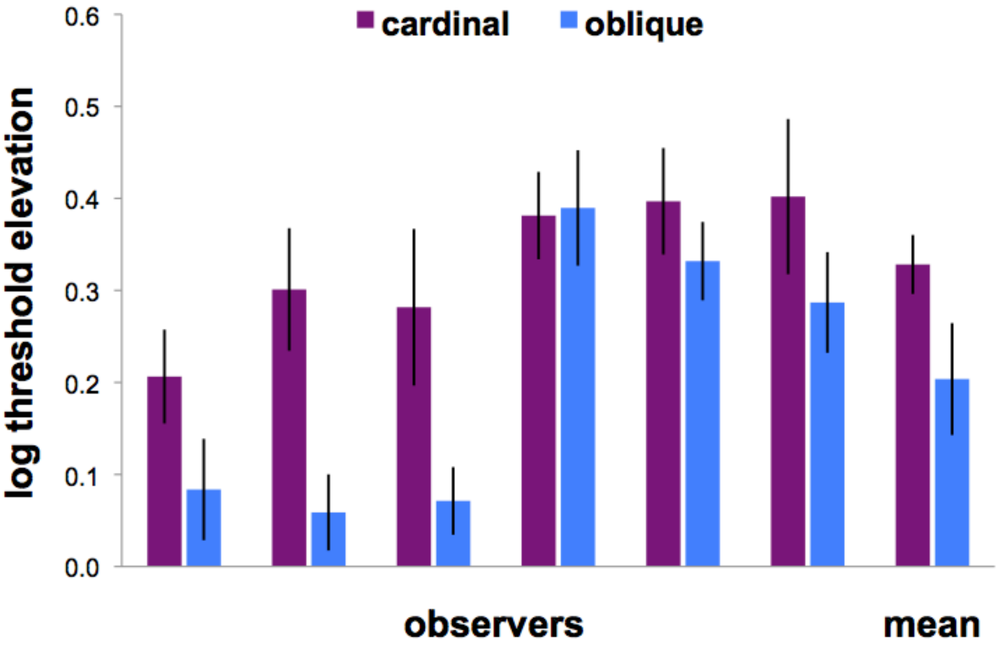

Figure 2.6: Results of Experiment 2.2. Plotted is the log threshold elevation in probe detection as a result of suppression of the pedestal stimulus, which was composed of orientation bandpass filtered noise. Data for the two cardinal conditions were averaged as well as the two oblique conditions. The bars on the farthest right denote the mean elevation values across observers (remaining bars). Error bars on individual data represent 95% confidence intervals derived from non-parametric bootstrapped threshold estimates (5000 repetitions, Efron & Tibshirani, 1993) and error bars on group data represent SEM.

In Experiment 2.2, contrast thresholds were measured for orientation bandpass filtered noise stimuli that were suppressed with CFS. Results indicate that sensitivity of cardinal orientations is more greatly impaired than sensitivity of oblique orientations. Previous studies found that suppression exhibits broad orientation-tuning of the suppressed stimulus (Ling & Blake, 2010; Stuit et al., 2009). The current results extend these findings by showing suppression with CFS is not uniform across all orientation components.

These results are consistent with the suppressive effects generated by dichoptic masking. The suppressive effects of the mask are mediated by the similarity in orientation between the mask and target; the strongest impairment in sensitivity occurs when the mask and target are identical in orientation (e.g. Baker & Meese, 2007; Harrad & Hess, 1992; Levi, Harwerth, & Smith, 1979). It has been further suggested that binocular rivalry and dichoptic masking are subserved by the same interocular suppression mechanisms (e.g. Baker & Graf, 2009; Sengpiel et al., 1995a; van Boxtel, van Ee, & Erkelens, 2007).

General discussion of Chapter II

Experiment 2.1 and 2.2 measured contrast threshold elevation due to CFS as a function of the spatial frequency and orientation features of the suppressed stimulus. Observers' sensitivity towards low spatial frequency information was more greatly impaired relative to high spatial frequency components. Moreover, stimulus patterns composed of horizontal and vertical features were more strongly suppressed in comparison to obliquely oriented stimuli. These findings together imply that input signals to the suppressed eye are not only weakened by suppression but those signals may undergo a filtering process, possibly leading to an altered neural representation of the suppressed stimulus. Such a claim has significant implications for previous CFS studies that rely on the intact neural representation of the suppressed stimulus as the basis for their claims (see Main Discussion).

A ready explanation for the results of Experiment 2.1 and 2.2 can be found when considering the spatio-temporal profile of the stimulus used to produce

CFS. Figure 2.7b shows the average 2D Fourier representation of 20 Mondrian patterns like those used in the current design (taken from Hong & Blake, 2009). Plotted is the amplitude spectrum, which characterizes the distribution of signal energy among different spatial frequencies and orientations. As illustrated, the effective spectral power of these commonly used Mondrian patterns mostly reside in its low spatial frequency components and particularly within the horizontally and vertically oriented contours (Figure 2.7c). This is not surprising given the composition of the CFS stimulus (i.e. high contrast rectangles, Figure 2.7a). Coincidently, Experiments 2.1 and 2.2 show that these particular components (i.e. low spatial frequencies and cardinal information) are most strongly suppressed by CFS. One could conclude that the selectivity and magnitude of suppression are modulated by the “strongest” spatial elements of the CFS stimulus. Detectors tuned to the features of the suppressor may selectively inhibit detectors responding to the same features in the suppressed stimulus; inhibitory strength would be directly related to the strength of input to those detectors. Because the spectral attributes of the CFS display used in these experiments consisted mostly of low spatial frequency and cardinally oriented components, corresponding feature detectors were optimally tuned to suppress neural responses to those same properties in the suppressed stimulus. Thus it follows that changing the spatial frequency and/or orientation content of the CFS stimulus should consequently alter the pattern of suppression. The following chapter describes experiments that directly address this question.

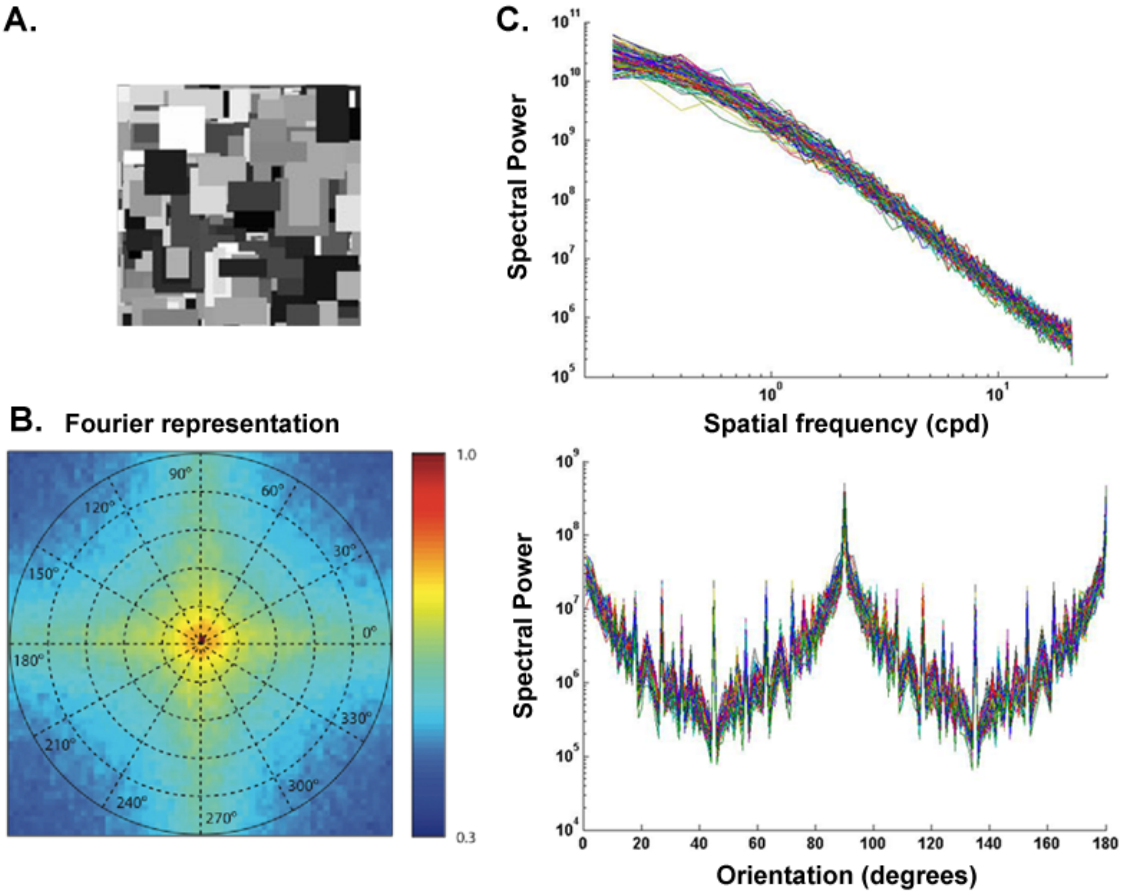

Figure 2.7: Fourier analysis of currently used CFS display. A) Example Mondrian image from a CFS display. B) Adapted from Hong & Blake (2009). Mean amplitude spectrum of 20 achromatic Mondrian images represented in the Fourier domain. Colors depict energy normalized to the DC value at different spatial frequencies and orientations, which are denoted by the distance from the origin and polar angle, respectively. C) Separate plots of the power (amplitude$^{\wedge 2}$) spectra for spatial frequency (top) and orientation (bottom) components of 100 achromatic Mondrian images (different colored lines).

CHAPTER III

MODULATION OF SUPPRESSION BY THE SPATIO-TEMPORAL FEATURES OF THE CFS DISPLAY

It is natural to assume that, during binocular rivalry, the strength of suppression exerted by one rival stimulus on the other rival stimulus depends on the relative strengths of the two. In terms of contrast, this turns out to be true: a high contrast CFS display produces significantly larger elevations in probe detection thresholds than does a low contrast CFS display. But to what extent is the effectiveness of CFS dependent on the particular stimulus components forming that display? There are some hints in the literature that the similarity between CFS and probe stimuli should matter. For example, Alais and colleagues (2006 & 2007) found that binocular rivalry suppression was stronger when the dominant stimulus shared similar features with the suppressed stimulus. Also, Hong and Blake (2009) found that chromatic CFS displays impaired the ability of observers to identify the color of a suppressed stimulus whereas achromatic CFS displays did not. If the spatial features of the suppressor indeed influence the depth and selectivity of suppression, this could provide clues as to why CFS is so effective and, more specifically, reveal the nature of information that is processed under interocular suppression.

Results presented in Chapter II show that CFS differentially impairs sensitivity to spatial frequency and orientation components of the suppressed stimulus. The experiments described in this Chapter ask the complementary question, namely do variations in the spatial frequency and temporal frequency components of the CFS display impact suppression depth as gauged by observer's contrast sensitivity for detecting the suppressed stimulus? To distinguish the effects of different spatial and temporal frequencies comprising the CFS display, Mondrian images were passed through a bandpass filter that preserved a given band of frequencies while rejecting frequencies outside this band. For Experiment 3.1, contrast detection thresholds for 5 spatial frequency gratings were measured as a function of the spatial frequency band of the filtered CFS display.

Experiment 3.1: Spatial frequency properties of the suppressor

Method

Stimuli

The suppressed stimulus was an annular sinusoidal grating (radius=1.4°), the spatial frequency of which was 0.75, 1.5, 3, 6 or 12 cpd. As in Experiment 2.1, the grating was oriented either 10° clockwise or counter-clockwise of vertical and its orientation and phase were randomly selected across trials. The edges of the annulus were spatially smoothed using a Gaussian filter. The grating was embedded in 1D broadband Gaussian noise (4° x 4°, 15% RMS contrast) to prevent baseline thresholds from reaching the floor and to increase task difficulty.

The CFS displays (4° x 4°; 10 Hz) were Mondrian-like patterns (rectangle length between 0.5°-1.4°) that were generated in an identical manner to those used in the experiments in Chapter II. In 5 of 6 CFS conditions, the CFS display was spatial frequency bandpass filtered through following steps. The 2D Fast Fourier Transform (FFT) was used to represent each image in the Fourier domain (Figure 2.7b). A radial bandpass filter (i.e., 2D Finite Impulse Response filter smoothed with a Butterworth filter to minimize artifacts) was applied to each Fourier transformed image, such that the radial distance from the origin was directly proportional to the desired spatial frequency range. The center frequencies for the bandpass filters were 0.75, 1.5, 3, 6 or 12 cpd (identical to the frequencies of the grating stimuli) with an octave wide bandwidth (Figure 3.1). The desired spectral components were also scaled in order to equate spectral density across different bandpass filtered images. The DC component was set to 0 prior to the filtering process and afterwards rescaled to mean luminance before the resulting filtered image was inverse Fourier transformed. All bandpass filtered and unfiltered Mondrian images were normalized in mean luminance (15 cd/m^2) and RMS contrast (General Methods). Prior to each block of a given CFS spatial frequency bandpass condition, one thousand CFS images were generated and 6 images were randomly sampled for each trial.

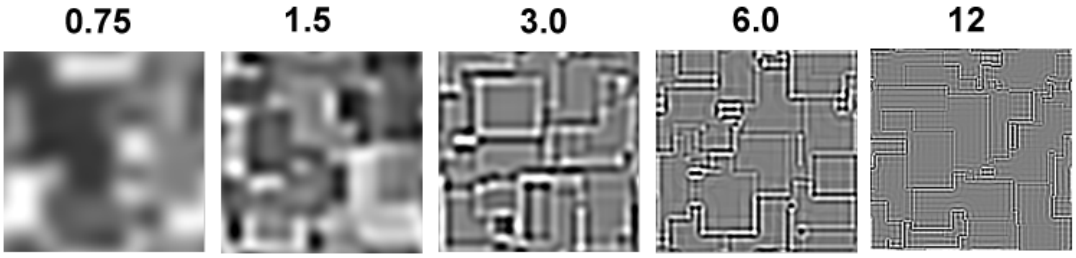

Figure 3.1: Examples of spatial frequency bandpass filtered Mondrian images. Values denote center spatial frequency (cpd) of each octave-wide bandwidth filter.

A mask image (4° x 4°) composed of randomly generated black and white (93.6 cd/m^2) pixels was presented at the end of each trial. Binocular fusion contours surrounding the stimuli and fixation dots were presented at all times to promote stable binocular eye alignment. Stimuli were presented against a homogenous field at mean luminance (15 cd/m^2).

Procedure

The procedure was similar to Experiment 2.1. A trial began with the dioptic presentation of binocular fusion contours and a fixation dot for 200 ms. During each trial, a grating stimulus of a given spatial frequency and orientation was presented to one eye while the other eye viewed either a blank field at mean luminance (baseline) or a dynamic CFS display (10 Hz) of a given spatial frequency range in the corresponding retinal position. The contrast of the grating linearly increased from 0 during the initial 300 ms in order to avoid abrupt transients. The grating remained at a set contrast predetermined by a staircase procedure for the remaining 300 ms of the trial. The stimuli were immediately replaced by a mask image in order to reduce possible negative afterimages and to indicate to observers that a response should be made. Observers performed a

2AFC orientation discrimination task, indicating whether the grating was oriented clockwise or counter-clockwise relative to vertical. Feedback was given once a response was made and the subsequent trial began after 1 s.

The experiment was separated into 6 sessions, each performed on separate days. The first session was devoted to measuring baseline contrast threshold estimates for orientation discrimination when the grating stimulus was presented without CFS. The remaining sessions measured threshold estimates in the presence of a CFS display. Gratings of 5 given spatial frequencies (0.75, 1.5, 3, 6 and 12 cpd) were presented in every combination with CFS displays of 6 different bandpass spatial frequency ranges (center frequency at 0.75, 1.5, 3, 6 and 12 cpd), including an unfiltered or all bandpass version. The 30 conditions were separated into 5 sessions such that each grating condition and each CFS condition were presented at least once within a session. Trials for each condition in a session were blocked and the order of conditions was randomized across sessions. The QUEST adaptive staircase procedure (Watson & Pelli, 1983) was implemented to obtain efficient estimates of contrast thresholds corresponding to 75% accuracy in performance. A block of trials (each condition) consisted of 4 randomly interleaved staircases (40 trials per staircase); half of the staircases measured threshold estimates for detecting a grating viewed by a given eye. When an individual’s threshold estimates did not properly converge, additional thresholds were obtained in another session. Practice trials were performed prior to the first and second sessions. Each session was approximately 45 minutes long and the experiment took about 5 hours to complete.

Results & Discussion

For every condition that involved CFS, a threshold elevation index was calculated as the log ratio of the mean threshold estimate for detecting a grating of a given spatial frequency under CFS to the mean baseline threshold estimate for detecting that same grating without CFS. Using this threshold elevation index, one can directly compare the suppressive effects of different bandpass filtered CFS displays on the detection of different spatial frequency gratings. Threshold elevation indices were entered into a 6 (CFS spatial frequency range) x 5 (grating spatial frequency) repeated measures ANOVA. The main effect of CFS spatial frequency ($F(5,10)= 26.4$, $p<.001$, $\eta_p^2=0.93$) and grating spatial frequency ($F(5,10)=23.1$, $p<.001$, $\eta_p^2=0.92$) was significant. Most importantly, the interaction between the spatial frequency of the CFS and grating stimuli was significant.

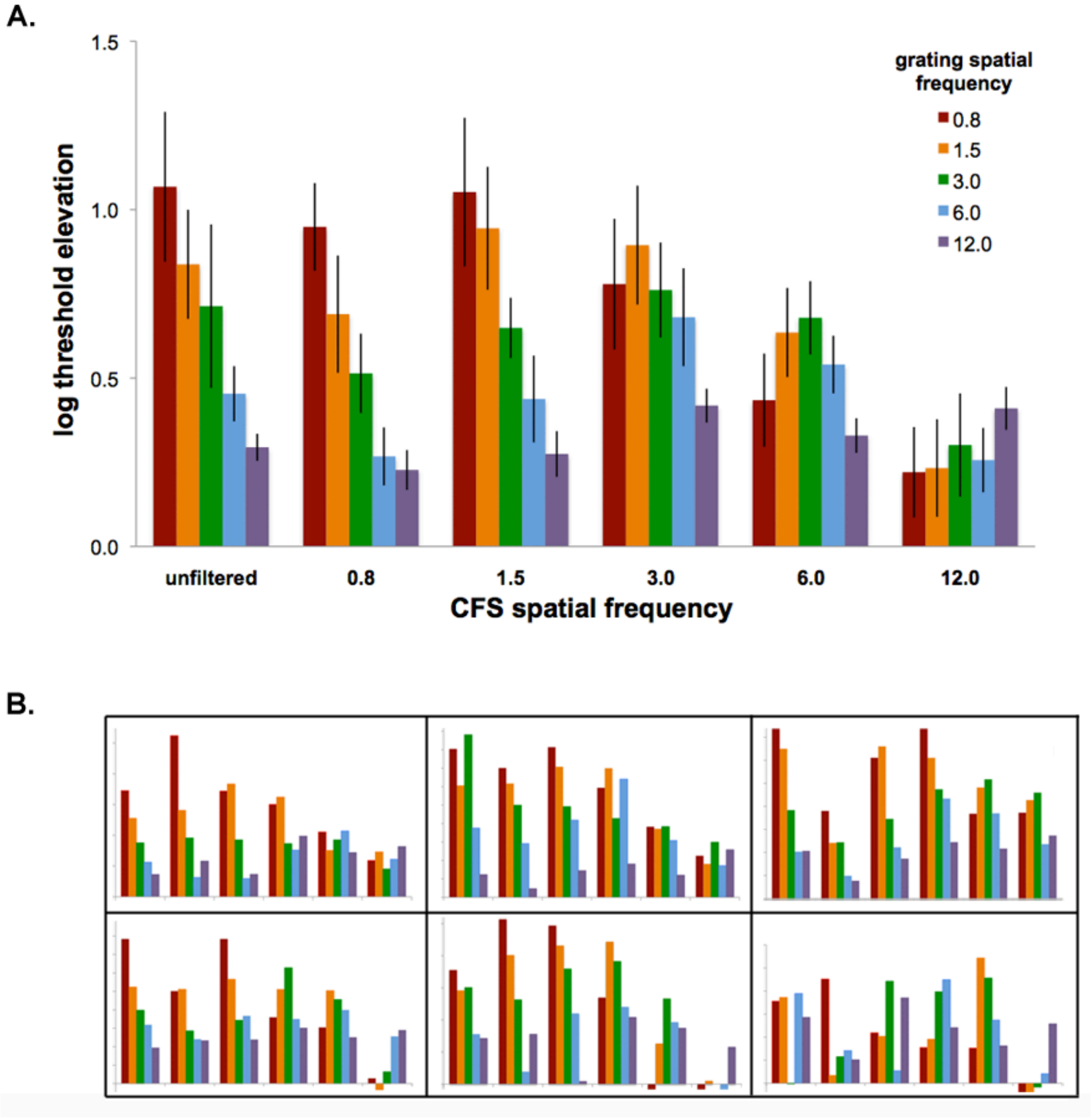

Figure 3.2: Results of Experiment 3.1. Group (A) and individual (B) mean elevation values in contrast thresholds for detecting a grating with a given spatial frequency (different color bars) is plotted as a function of the CFS (center) spatial frequency. Error bars denote SEM.

Figure 3.2 shows the pattern of threshold elevations for each of the 5 spatial frequency gratings (denoted by different colored bars) as a function of different bandpass filtered CFS displays (center frequency values expressed on the horizontal axis). Several features of these results stand out. First, the unfiltered CFS display produced higher threshold elevations (i.e. lower contrast sensitivity) as the grating spatial frequency decreased, replicating the results from Experiment 2.1. A similar pattern in threshold elevation occurred with low bandpass filtered CFS displays with center frequencies of 0.8 cpd and 1.5 cpd; the interaction between CFS condition (unfiltered vs. 0.8 cpd; unfiltered vs. 1.5 cpd) and grating spatial frequency was not significant (*ps*> 0.5). As the center frequency of the CFS bandpass filter increased, however, the bias towards higher threshold elevations for low spatial frequency gratings disappeared; the interaction between CFS and grating spatial frequency reached significance (unfiltered vs. 3 cpd: F(4,20)=2.3, p=.09, η_p^2=0.3; unfiltered vs. 6 cpd: F(4(20)=7.3, p=.001, η_p^2=0.6; unfiltered vs. 12 cpd: F(4,20)=11.1, p<.001, η_p^2=0.7). Moreover, overall threshold elevations were reduced relative to the unfiltered CFS condition particularly for the highest bandpass filtered condition (12 cpd: t(5)=4, p=.01), which suggests that this filtered CFS display evoked relatively weak suppression despite the fact that it was equivalent in spectral density as that of the unfiltered CFS display. In addition, this pattern of results obtained in Experiment 3.1 was replicated with 2 new observers and the author in a separate experiment using a smaller stimulus display (2° x 2°), longer stimulus duration (1.6 s), and a different range of spatial frequency gratings and CFS bandpass filters (Appendix B).

The results from Experiment 3.1 confirm that information composed of low spatial frequencies is more strongly suppressed than high spatial frequency information by CFS. Furthermore, the pattern in threshold elevation observed with unfiltered CFS can be reproduced using CFS displays composed solely of low spatial frequency information. As mentioned previously, the effective spectral power of these commonly used Mondrian patterns mostly resides in its low spatial frequency components, which is apparent in the average 1D Fourier power spectrum illustrated in Figure 2.7. Thus, the potent suppression produced by CFS may be mainly attributable to the energy residing in its low spatial frequency components. This is also consistent with the result that CFS composed mainly of high spatial frequencies was relatively less effective at producing strong suppression. Mean threshold elevation with high bandpass filtered CFS (center frequency of 6 cpd or 12 cpd) was in the range of 0.3 - 0.5 log units, which is more similar to the sensitivity loss reported with binocular rivalry (e.g. Blake et al., 2006; Nguyen et al., 2001; Wales & Fox, 1970) than with CFS (Tsuchiya et al., 2006). Thus, high spatial frequency components of the CFS display may contribute little to its potency.

Altogether these findings suggest that the depth and selectivity of suppression are dependent upon the spatial components of the suppressor as well as those of the stimulus being suppressed. As mentioned previously, neural units tuned to the features of the suppressor may selectively inhibit units responding to the same features in the suppressed stimulus, with the strength of inhibition modulated by signal intensity. Y. Yang, Rose, and Blake (1992) found that rivalry was most prominent with dissimilar patterns that were matched in spatial frequency content and especially within the low spatial frequency range (also Hollins & Hudnell, 1980; O’Shea, Sims, & Govan, 1997). Consistent with this are the findings with the unfiltered, low (0.8-1.5 cpd), and mid-range (3-6 cpd) bandpass filtered CFS stimuli: suppression depth peaks at the grating spatial frequency that is roughly consistent with the center frequency of CFS filter. However, this claim cannot explain the relatively weak and non-selective suppression of high spatial frequency information by high (12 cpd) bandpass filtered CFS (one way ANOVA: $p>.05$). This shallow suppression may reflect a non-linear component of the suppression mechanism such that not all feature detectors are equally effective at producing CFS, as alluded to earlier. Consistent with this, Y. Yang et al (1992) also reported that stimuli sharing the same high spatial frequency content were readily perceived as superimposed on one another whereas transparency was observed when competing stimuli differed in spatial frequency information, especially when one stimulus was of high spatial frequency. High spatial frequency detectors, in general, may prove to be weak at inducing interocular suppression. While it is possible that selectivity may be harder to identify with weak suppression, there may be another component that contributes to the broad suppression produced by high spatial frequency detectors. It is possible that such a component may be evidenced in the temporal frequency domain, and it is to that possibility that we turn to next.

Experiment 2.2: Temporal properties of the suppressor

Introduction

Experiment 2.2 examines whether the temporal characteristics of CFS influence its effectiveness in perceptually suppressing stimuli. It is well established that a moving stimulus tends to dominate in rivalry over a stationary stimulus (Blake, Zimba, & Williams, 1985; Wade, de Weert, & Swanston, 1984) and motion speed can modulate suppression durations during BR (Blake, Yu, Lokey, & Norman, 1998; Fox & Check, 1968). Unlike the typically smooth and predictable motion implemented in BR studies (e.g. random dot cinematogram), CFS usually involves a continuous onset of brief stimulus transients together with abrupt changes in shape edge and contrast. These temporal events plausibly contribute to the deep suppression evoked by CFS, but it is unclear how.

The multiple flashes presented during CFS may lead to the culmination of inhibitory signals that evoke perceptual suppression. Indeed, the onset and offset of a stimulus generates strong excitatory and inhibitory signals, which can render a stimulus perceptually invisible (Macknik & Livingstone, 1998; Macknik, Martinez-Conde, & Haglund, 2000). Wen and Zhang (2009) reported long-lasting cortical responses (>1 s) to monocular transients produced by flash suppression in cat area 18. Furthermore, the inhibitory activity correlated with stimulus onset and offset may originate from neurons whose receptive fields correspond to the spatial edge of a stimulus (Macknik & Haglund, 1999). Moreover, Tsuchiya et al. (2006) showed that CFS was most effective when there were at least 5 consecutive flashes in a CFS display.

The flash interval alone is also found to be another important parameter for reliable suppression. Tsuchiya and Koch (2005) found that flash rates between 3-12 Hz (80-320 ms flash intervals) were most effective at producing long suppression phases of the competing stimulus (see also Arnold et al., 2008). Most studies to date continue to present CFS patterns at 10 Hz; however, some (~30%) use higher rates that may not produce such potent suppression (e.g. Bahrami et al., 2008 & 2010, Jiang et al., 2009; Sterzer et al., 2008 & 2009). Interestingly, the temporal frequency range (3-12 Hz) typically employed with CFS resonates well with the human spatio-temporal contrast sensitivity function, which reaches maximum sensitivity at approximately 5-15 Hz (Kelly, 1969 & 1974).

Method

Stimuli

For every trial, 10 gray-scale Mondrian-like patterned images (5° x 5°) were randomly generated to produce a CFS display in which each image repeated for 10 consecutive frames (10 Hz) in a 100-frame sequence (1 s). The time-series in luminance change for every pixel within a CFS display was fast Fourier transformed and bandpass filtered in the temporal frequency domain by removing the sinusoidal components either 10 Hz and below (high-pass) or above (low-pass) 10 Hz (Figure 3.3). To account for anisotropies in the temporal amplitude spectrum of the original (unfiltered) time-course, the amplitudes of the remaining temporal components were scaled such that spectral densities were equated across different bandpass filtered sequences. The DC component was set to 0 in the beginning of the temporal filtering process and afterwards rescaled to mean luminance (15 cd/m^2) before the resulting filtered spectrum was inverse

Fourier transformed. The image sequence was then normalized in mean luminance and RMS contrast.

The suppressed stimulus was a noise patch (5° x 5°; 15% RMS contrast) that was spatial frequency bandpass filtered in the Fourier domain using a 2D Finite Impulse Response filter and smoothed to reduce aliasing. The spatial frequency band of the noise patch was centered at 1.5 cpd or 8 cpd with an octave-wide bandwidth. The probe was a contrast increment (1.6° x 4.3°) that occurred above or below fixation. The probe emerged and disappeared gradually following a Gaussian contrast ramp to avoid abrupt onset transients. The contrast at the edges of the probe was also spatially smoothed using a Gaussian filter to reduce the perception of edges produced by abrupt differences in contrast.

A mask image (5° x 5°) was presented to both eyes at the end of each trial and was randomly composed of black and white (93.6 cd/m^2) pixels. Binocular fusion contours surrounding the stimuli and fixation dots were presented at all times to promote stable binocular eye alignment. Stimuli were presented against a homogenous field at mean luminance (15 cd/m^2).

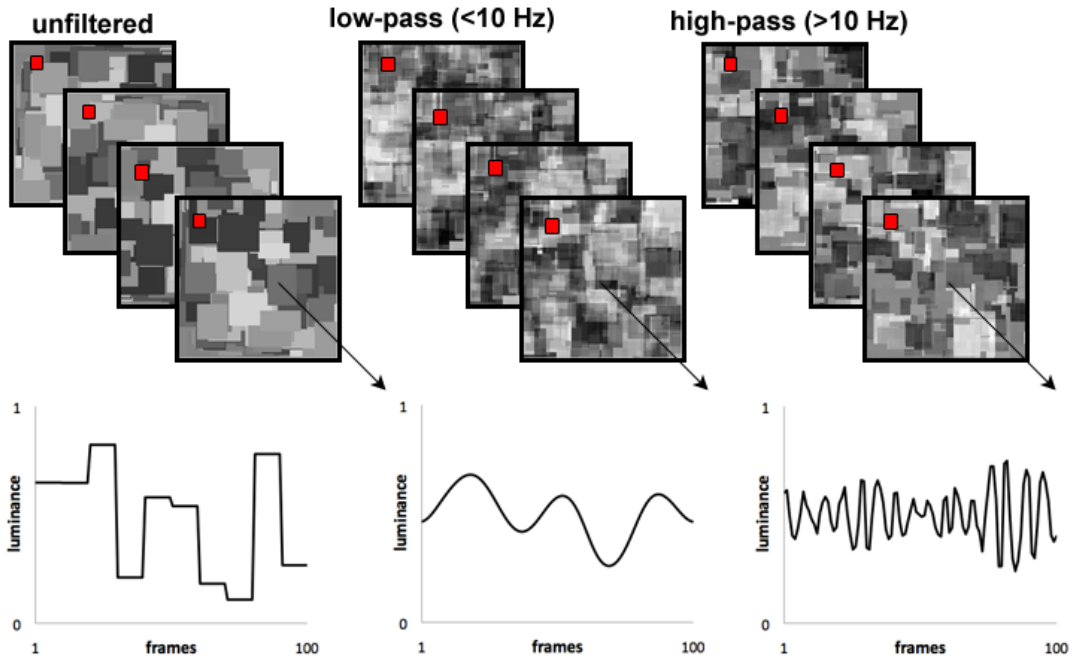

Figure 3.3: Illustration of the outcome of temporal bandpass filtering. Top images represent example Mondrian images that were unfiltered, low-pass filtered, or high-pass filtered. Bottom images depict the luminance change across time (100 frames) for a given pixel (red) within the CFS display above.

Procedure

In the beginning of a trial, the pedestal stimulus was presented to one eye while a CFS display or gray uniform field, depending on the session, was presented to the corresponding retinal position of the other eye. To allow for the potential accumulation of suppressive effects produced by successive flashes (Tsuchiya et al., 2006), the probe was introduced 500 ms after trial onset (after 5 flashes) and gradually emerged and disappeared for 500 ms (peak at 250 ms). The probe randomly appeared either above or below fixation. The contrast increment was determined by a staircase procedure. The stimuli were immediately replaced by a mask image dioptically in order to reduce possible negative afterimages and to signal to observers that a response should be made.

Observers performed a 2AFC detection task, indicating the location of the probe relative to fixation. Feedback was given once a response was made and the subsequent trial began after 2.5 s.

The experiment consisted of 3 sessions in which contrast thresholds were estimated for detecting low and high spatial frequency bandpass filtered probe stimuli. The first session obtained baseline measurements in which CFS was absent and also served to acclimate observers to the task and stimuli. In the remaining sessions, CFS displays were either low temporal bandpass filtered, high temporal bandpass filtered or unfiltered. Each temporal CFS condition was paired with each of the 2 spatial frequency filtered probe stimuli, resulting in 6 different conditions. Trials for each condition were blocked and two staircases were randomly interleaved within each block. All conditions were equally presented in each session. Four threshold estimates corresponding to 71% performance were obtained for each condition using a 2 Down-1 Up staircase procedure (Levitt, 1971). When an individual's threshold estimates did not properly converge, additional thresholds were collected. Practice trials were performed prior to each session and the experiment took approximately 2.5-3 hours to complete.

Results & Discussion

As done in the previous experiments a threshold elevation index was calculated for each of the 6 conditions as the log ratio of the mean threshold estimate for detecting a given spatial bandpass filtered probe under a given CFS temporal frequency condition to the mean baseline threshold estimate for detecting that same probe without CFS (Figure 3.4). The elevation indices were then entered into a 3 (CFS temporal filter) x 2 (probe spatial frequency) repeated measures ANOVA. The main effects of probe condition (F(1,5)=11.1, p=.02, η_p^2=0.7) and CFS condition (F(2,10)=7.4, p=.01, η_p^2=0.6) were statistically significant, but the interaction between the two was not. Consistent with previous experiments, CFS again produced nearly 3 times greater threshold elevation for detecting low spatial frequency probes (0.25 ± 0.04) in comparison to high spatial frequency probes (0.09 ± 0.02). A CFS display that consisted of low temporal components (including its fundamental frequency) was as effective at suppressing high (0.09 ± 0.02) and low spatial frequency probes (0.27 ± 0.03) as an unfiltered CFS display (high: 0.13 ± 0.03; low: 0.28 ± 0.02; *ps*>.05). However, a CFS display that consisted of only high temporal components was not as effective at suppressing high (0.03 ± 0.02, p=.03) and low spatial frequency probes (0.19 ± 0.06. p=.08) in comparison to an unfiltered CFS display.

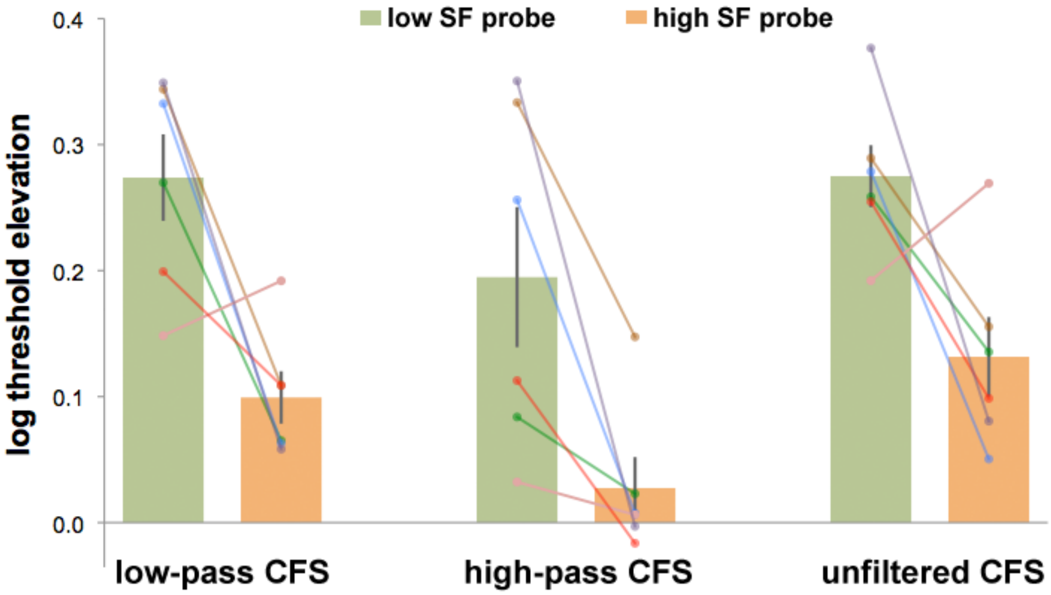

Figure 3.4: Results of Experiment 3.2. Plotted are the threshold elevations in detecting a low (green) or high (orange) spatial frequency (SF) bandpass filtered probe stimulus that is suppressed with either a temporal low-pass, high-pass, or unfiltered CFS display. Lines of different colors denote individual data. Error bars represent SEM.

When an unfiltered sequence of CFS images is presented, a given pixel may abruptly change luminance from frame to frame, which in this case is every 100 ms or 10 Hz. Those sharp luminance changes over time produce a broad spectrum of temporal frequencies, which peak at 10 Hz. A CFS display that includes only the low temporal components of that distribution appears smooth in transition but nonetheless, is as effective in suppression as an unfiltered CFS display, according to the results of Experiment 3.2. This is most likely attributable the energy concentrated near and at the peak of the CFS temporal spectrum (10 Hz), which also happens to be the peak of the human temporal contrast sensitivity curve under scotopic conditions (5-10 Hz; Kelly, 1961). On the other hand, a CFS display that consists of energy only within the high temporal frequency range (> 10 Hz) of the unfiltered CFS spectrum appears to have frequently abrupt transitions and yet is less effective at producing strong suppression. Thus, the relatively high temporal frequency components in an unfiltered CFS display contribute less to suppression than do the low frequency components.

In addition, the relative bias in suppression for low spatial frequencies is still observed with both low and high-pass temporal filtered CFS displays. It is possible that the temporal characteristics of CFS further increase the imbalance in suppression of the spatial frequency domain beyond that of its spatial properties. This would explain the results from Experiment 3.1 in which there was residual suppression of low spatial frequencies by the high spatial frequency bandpass filtered CFS. However, since the natural spatial profile of the CFS stimulus was preserved across all conditions (i.e. energy was concentrated mostly in low spatial frequencies), it is difficult to determine to what extent the temporal profile of CFS contributed to the low spatial frequency bias in suppression in the current experiment.

It is well known that the frequency at which a stimulus flickers or changes in velocity modulates the visual system's sensitivity to the spatial frequency content of that stimulus (e.g. Kelly, 1961 & 1969; Kulikowski & Tolhurst, 1973; Robson, 1966). As temporal frequency increases, contrast sensitivity to spatial frequencies changes from bandpass to low-pass. That is at low temporal frequencies (<5 Hz), contrast sensitivity to low and high spatial frequencies is relatively weak when compared to intermediate spatial frequencies around 2-6 cpd where sensitivity is best. At higher temporal frequencies, sensitivity to low spatial frequencies is enhanced and sensitivity to high spatial frequencies is depressed. Such dichotomy in spatiotemporal sensitivity corresponds well with response profiles of cells residing in the magnocellular (M) and parvocellular (P) pathway (e.g. Livingstone & Hubel, 1988; Maunsell & Van Essen, 1983; Ungerleider & Mishkin, 1982). P cells are sensitive to stimuli with high spatial frequency and low temporal frequency characteristics and exhibit a sustained or tonic response throughout the stimulus duration (e.g. Fukuda & Saito, 1971; Kaplan & Shapley, 1986). M cells exhibit transient, or phasic, responses to the onset and offset of stimuli comprising low spatial frequency and high temporal frequency components (e.g. Kaplan & Shapley, 1986; Wilson, 1980).

Therefore, one could surmise that the spatiotemporal properties of the currently utilized (unfiltered) CFS displays - predominately low in spatial frequency content with high temporal frequency flicker - may stimulate M cells more effectively than P cells. On the other hand, a dynamic CFS display with properties that weakly stimulate one or both pathways - low spatial frequency contours flashing at low or very high temporal frequencies - may be less effective at suppressing a competing stimulus. Thus it may not be so surprising that the temporal high-pass filtered CFS condition (temporal components ranging from 20-50 Hz) failed to produce strong suppression. Moreover, Tsuchiya and Koch (2006) showed that dominance durations for a flashing stimulus decline as the flash interval is shortened below 100 ms, as is the case for the temporal high-pass CFS condition. In subsequent studies it would be informative to dissociate the suppressive effects of different temporal components at a finer resolution and include a static condition (one CFS frame) for comparison.

CHAPTER IV

GENERAL DISCUSSION

The use of continuous flash suppression has become increasingly popular in the last decade, especially for the study of unconscious visual processing. Investigators have exploited the strong and sustained suppression produced by CFS to determine whether select classes of visual input continue to be registered without awareness. There is indeed ample evidence to suggest that certain types of information can be encoded from a suppressed stimulus, such as its semantic and emotional content (review by Lin & He, 2009). It may be easy to conclude that the processing of certain ‘meaningful’ classes of stimuli is unaffected by CFS and is thus ‘unconscious’ in nature. However, it is also possible that CFS differentially suppresses local features common to a stimulus class; effects that are presumably driven by the encoding of high-level attributes may, in fact, be driven by visual properties that are only weakly affected by CFS. The objective of this dissertation was to understand what CFS is actually suppressing so that more accurate conclusions can be drawn about the nature of the information that is processed under CFS.

This study investigated whether the spatio-temporal properties of a CFS display contribute to its effectiveness as a potent suppressor. Experiments in Chapter II explored the selectivity and depth of CFS within the spatial domain. Experiments in Chapter III examined the role of select feature dimensions of CFS in producing such patterns in suppression. Suppression depth was determined by elevations in contrast detection thresholds to stimuli as a result of suppression and was measured as a function of the spatial frequency (Experiment 2.1) and orientation (Experiment 2.2) of the suppressed stimulus and the spatial frequency (Experiment 3.1) and temporal frequency (Experiment 3.2) of the suppressor. Experiment 2.1 and 2.2 showed that CFS was biased at suppressing certain components in the spatial frequency and orientation domains: sensitivity was significantly impaired for information in the low spatial frequency range (<4 cpd) and at the cardinal orientations. These are also the same components that are most strongly represented in the CFS stimulus itself. To determine whether this pattern in suppression can be attributed to the spatio-temporal properties of the CFS stimulus, in Experiment 3.1 and 3.2 sensitivity measurements were repeated but using CFS stimuli composed of select spatial frequency or temporal frequency components. Results from Experiment 3.1 showed that low spatial frequency bandpass filtered CFS can reproduce the suppression bias for low spatial frequencies previously observed with unfiltered CFS. However as the CFS spectral profile shifted towards higher spatial frequency ranges, this bias in suppression disappeared and suppression became shallow. Similarly in Experiment 3.2, temporally low-pass filtered CFS produced the same selectivity and depth in suppression as temporally unfiltered CFS. High-pass CFS produced similar patterns in selectivity for low spatial frequencies but suppression was shallower in general.

Altogether this pattern of findings suggest that CFS differentially impairs the processing of stimulus features and the magnitude and selectivity of suppression is modulated by the spatio-temporal features predominant in the CFS stimulus - in this case, low spatial frequency, cardinally oriented spatial components and temporal components of 10 Hz and lower. These findings have several important implications. For one, they support the growing evidence that suppression is not completely non-selective in nature. Not only is the neural representation of a stimulus weakened by CFS, but it may also be significantly altered under suppression. Secondly, the low-level features of the suppressor and suppressed stimulus may be what determine suppression selectivity and thus the nature of information that is processed under suppression. This questions whether the previously reported effects with CFS were entirely attributable to the preferential processing of meaningful stimulus attributes. Finally, these findings implicate the involvement of feature selective mechanisms during suppression and may alter our current conception of the neural framework underlying binocular rivalry. Such implications are discussed in detail below.

Suppression includes a feature-selective component

There is a widely held view that rivalry suppression non-selectively weakens all visual signals to the suppressed eye (review by Blake & Logothetis, 2002). In other words, suppression is impartial to the content of information presented to the suppressed eye and thus neural signals evoked by different stimuli and stimulus properties are all effectively attenuated under suppression, gating the flow of input to subsequent processing stages. However, evidence for this view has relied on early psychophysical evidence showing that probe targets briefly superimposed on a rival stimulus presented to one eye were harder to detect when that rival stimulus was suppressed. Impairments in detection were found regardless of the kind of probe presented (e.g., flashes of light, letters) and regardless of the similarity of that probe to the suppressed stimulus itself (e.g. Fox & Check, 1966; Wales & Fox, 1970; review by Blake, 2001). Impaired detection, in other words, generalized to essentially all new stimulation introduced to a suppressed eye, leading to the notion that suppression operates non-selectively. Note, however, that those early studies were not performed in a way that provided a direct measure of the depth of suppression, and they did not claim that suppression was equivalent in magnitude for all types of probes regardless of their similarity to the suppressed stimulus itself.

More recent studies have systematically found that suppression is tuned to the features of the suppressed stimulus (e.g. Alais & Parker, 2006; Watanabe et al., 2004). For instance, Stuit et al. (2009) reported that suppression was strongest for probes that were close in orientation or spatial frequency to the suppressed stimulus. Changing those features in the suppressed stimulus has also been documented to break suppression (O’Shea & Crassini, 1981; Walker & Powell, 1979). Furthermore, suppression may deepen along hierarchical stages of analysis. Impairments in visual sensitivity worsen as the form and motion properties of a suppressed stimulus become more complex in nature (Ngyuen, Freeman & Alais, 2003; Li et al., 2005). Contextual illusions attributed to early visual processes (e.g. brightness contrast illusion) survive CFS whereas those same illusions and others (e.g. illusory contours with Kanizsa triangles) fail to show interocular transfer (Maruya et al., 2008; Cai, Zhou, & Chen, 2008; Kawabe & Yamada, 2009) or are abolished when higher computations are necessary (Harris, Schwarzkopf, Song, Bahrami, & Rees, 2011; also Sobel & Blake, 2003). Finally, there is some indication that suppression naturally inhibits the processing of certain stimulus properties more so than others. Rivalry suppression greatly impairs color sensitivity in comparison to luminance sensitivity (E.L. Smith et al., 1982), and furthermore this impairment may be specific for certain ranges of wavelengths (Ooi & Loop, 1994 but Nguyen et al., 2001). Importantly, Hong and Blake (2011) showed that differential suppression of chromatic and achromatic mechanisms is dependent on the luminance properties of the suppressor: chromatic CFS displays weakened observers' color sensitivity whereas achromatic CFS displays did not. Along the same lines, Y. Yang and colleagues (1992) showed that rivalry occurred most readily with dissimilar patterns matched in spatial frequency content and especially within the low spatial frequency range. In comparison, stimuli of predominantly high spatial frequency content tend to produce non-rivalrous perception such as superimposition or transparency. In summary, selectivity in suppression has been observed in several different ways - in terms of the features of the suppressed stimulus and among the different stages of analysis. The current study underscores the importance of another type of selectivity in suppression that is defined by the stimulus properties of the suppressor and their interaction with the features of the suppressed stimulus.

The feature-selective impairment in contrast sensitivity observed with CFS resembles the attenuation in contrast sensitivity resulting from adaptation. Visual sensitivity to a test stimulus is significantly weakened after prolonged viewing of a stimulus matching in visual features (Blakemore & Campbell, 1969; Pantle & Sekuler, 1968). Furthermore, this adaptation effect occurs, although attenuated, when the adapting and test stimuli are presented to different eyes (e.g. Bjorklund & Magnussen, 1981; Blakemore & Campbell, 1969). There are several reasons to suggest that the current findings are unlikely a result of adaptation to the CFS display. The short trial duration (600-1600 ms) and continuous change in local features (every 100ms) of the CFS display reduces the odds for effective adaptation. For instance to obtain the threshold elevation equivalent for a 6 cpd grating suppressed with a CFS display of the same center frequency (~0.5 log units), based on previous studies, the adaptation duration would have to be on the order of 100 s if stimuli were presented to the same eye and 1000 s if they were presented to different eyes (Figure 3 of Bjorklund & Magnussen, 1981; also Greenlee, Georgeson, Magnussen, & Harris, 1991; Blakemore & Campbell, 1969). Furthermore, the impairment in sensitivity due to adaptation is limited to test stimuli ±1 octave from the adapting spatial frequency (e.g. K.K. De Valois, 1977), which is far more narrow than the impairment observed in the current study: a CFS display centered at 0.8 cpd was still effective in elevating thresholds for a grating of 12 cpd, for example. Rather, contrast sensitivity is reportedly enhanced for test stimuli that are 2 octaves away from the spatial frequency of the adapting stimulus (e.g. K.K. De Valois, 1977); however such enhancement was not observed in the current study. Finally, an adaptation effect would not explain the weak selectivity observed with high spatial frequency CFS displays.

Implications for past and future studies

Studies that utilized CFS typically compare the behavioral or physiological effects associated with the presentation of different stimulus categories during suppression. When differential effects are observed (e.g., face images are rendered ineffective but tool images are not), those effects are typically attributed to selective processing of high-level (e.g. semantic) properties under CFS. Results from these studies, in other words, are interpreted as evidence that certain classes of 'meaningful' information are preferentially processed in the absence of awareness, the implication being that such information has special functional significance. Take for example the behavioral study by Almeida et al. (2008 & 2010) in which objects of different categories (i.e. animals and tools) were presented as invisible prime images using CFS and visible target images. Observers' performance in discriminating targets was facilitated by primes of the same category, but this priming effect was only found with tool-related stimuli. It was reasoned that the manipulability factor behind tools allows this class of objects to be processed differently from other object categories. Since areas along the dorsal pathway purportedly respond best to tool-like images (Chao &

Martin, 2000; Fang & He, 2005), CFS was thought to disrupt activity mainly in ventral areas where other object categories were represented. Almeida's findings have been taken as direct evidence that dorsal processes have privileged access to unconsciously presented stimuli (Goodale & Milner, 1992; Stoerig & Cowey, 1997).

There is ample evidence that processing of low-level stimulus properties including contrast, orientation, and motion are significantly attenuated by CFS (e.g. Kanai et al., 2006; Maruya et al., 2008) and to an even greater extent than by conventional binocular rivalry (Tsuchiya & Koch, 2005). How, then, can advanced stages of analysis occur, such as discriminating object manipulability, despite disruption of low-level visual input? Lin and He (2009) proposed the *unconscious binding hypothesis*: "binding during unconscious processing is possible, albeit fragile: the brain can associate, group, or bind certain features in an invisible scene to form a certain cortical representation, and such binding can be detected under optimal conditions… binding is possible during unconscious processing if critical features can be registered and attentively grouped." It is unclear exactly how they define 'critical features' but it seems to depend on the extent to which the underlying neural mechanisms are affected by suppression (involved in consciousness). Based on findings by Almeida et al. (2008 & 2010; also Fang & He, 2005), critical features were bound to create the neural representation of manipulable objects that engaged dorsal processes outside of awareness (Lin & He, 2009).

An alternative account is that CFS differentially suppresses local features that define particular classes of objects, disrupting selective processing of those features and the effects (e.g., adaptation) associated with those classes of objects. While this account does not necessarily contradict the framework proposed by Lin and He (2009) - they acknowledge that only “critical” low-level features may be encoded - it suggests that neither the intact neural representation of the stimulus nor the engagement of specific high-level processes are necessary to produce the effects reported under CFS. This account would also imply that suppression mainly operates at early stages of processing, the consequence being that residual activity arising at later stages would be even less likely to occur because of the weakened feedforward input to those later stages (Nguyen et al., 2003).

Can this alternative account explain the selective priming results reported by Almeida et al (2008 & 2010)? The tool images that were used were all elongated and most were oriented in oblique directions. In contrast, animal images tended to be oval in shape and thus broad in terms of their orientation content. Perhaps, then, the priming effects with tool images were not driven by the correspondence in object category but rather the similarity in orientation content between the “invisible” tool images used for priming and the visible tool images used as targets. Furthermore according to Experiment 2.2, impairments in contrast sensitivity are relatively weak for obliquely oriented information. Perhaps this stimulus feature can evoke sufficient activity to drive priming effects of images sharing similar orientation. Furthermore, such priming may not be necessarily unconscious since such stimuli may be weakly suppressed and more likely visible to observers. If these results were evidence of orientation-specific priming rather than category-related priming, then logically priming effects should be found with other stimuli similar in orientation regardless of object category. For instance, elongated animals oriented in oblique directions should produce a priming effect whereas round shaped tools should not.

Yet another possibility is that the visual properties weakly suppressed by CFS - for example, high spatial frequency and obliquely oriented components - are unconsciously processed to an extent that they are sufficiently bound to create a weak stimulus representation. However if feature-specific tuning is broadened under suppression (Ling & Blake, 2010), it is likely that more complex representations are also altered as well. Nonetheless, this noisy representation may still activate high-level computations in which ‘meaningful’ information is extracted. Such an account is consistent with both the current findings and the framework by Lin and He (2009). The discrepancy arises in understanding why those features are processed and consequently why that representation is generated. Are the critical features of an object category processed under CFS because there is something special about the pathway by which that stimulus category is analyzed or because the visual properties of CFS stimulus led to weak suppression of those features? This would be easily resolved by examining whether results hold after: 1) equating or controlling for several low-level features that differ across stimulus categories, 2) using a CFS display that is composed of different visual properties or 3) using a CFS display that is relatively unbiased in feature suppression.

These different sources of effects can be extended to most studies utilizing CFS since nearly all have ignored the possibility of feature-selective suppression as a consequence of the type of stimuli used. CFS studies can be divided into two categories based on their technique and measure of interest. In one category, a stimulus is held under suppression and indirectly related to the measure of interest. The study by Almeida et al (2008 & 2010) falls in this category. In the second category, a stimulus is initially suppressed and the measure of interest is the time necessary for its emergence from suppression (i.e. suppression duration). In most cases, the contrast of the CFS display is slowly reduced while the contrast of the suppressed stimulus is increased during a trial in order to promote breakage and reduce trial durations. The idea is that stimuli emerging more quickly from suppression, as evidenced by shorter RTs, are more likely to have been processed under suppression.

Previous CFS studies using this “emergence from suppression” technique were typically looking for evidence of face or word processing without awareness. For instance, it is well documented that fearful faces emerge from suppression faster than do faces exhibiting other expressions (Gray, Adams, & Garner, 2010; Sterzer et al., 2011; Tsuchiya et al., 2009; E. Yang et al., 2007). The common interpretation is that affective processing occurs without awareness and, in particular, that fear-related facial expressions receive prioritized processing due to their biological significance. Yet this fear-related advantage in overcoming suppression also occurs with inverted faces (E. Yang et al., 2007) and inverted luminance-reversed faces, the latter of which substantially impair recognition of emotional expressions (Gray et al., 2010). Thus, it is entirely plausible that differences in low-level features may contribute to suppression's differential effect on facial expressions as indexed by their emergence from suppression. Indeed, categories of affective images may have some consistent differences in spatial frequency content (Delpanque, N'diaye, Scherer, & Grandjean, 2007). The discrepancies in spatial frequency profiles of fearful and neutral faces, however, are not well documented. Based on the current study, one could speculate that the rate of overcoming suppression is modulated by amplitude differences in high spatial frequency content, since high spatial frequencies are least impaired by CFS. Furthermore, this would argue against the involvement of the amygdala in stimulus detection since it is more responsive to low spatial frequency face information whereas fusiform activity is greater for the high spatial frequency content of faces (Vuilleumier et al., 2003). Results from an additional experiment (Appendix A) show that not only is suppression weaker for faces composed solely of high spatial frequencies, but these images break suppression faster in comparison to faces composed of only low spatial frequencies (after equating for differences in sensitivity). It is also well established that low spatial frequency stimuli tend to be suppressed longer than high spatial frequency stimuli (Arnold, Grove, & Wallis, 2007; Breese, 1909; Fahle; 1982; Levelt, 1965). Future studies would be wise to equate the spatial frequency content of images before measuring durations of suppression under CFS.

Another concern regarding this second category of CFS studies is whether they were examining effects that were driven by the stimulus when it was *invisible*. Authors of these studies claim that the differences in suppression duration must be indicative of the rate at which the stimulus is processed unconsciously: a stimulus that breaks suppression faster must have been processed faster under CFS. On the other hand, accurate performance on a detection task requires that the stimulus be processed to some extent on a conscious level. Secondly, the discrepancy may occur at a decision-making level rather than at the level of stimulus processing. Modeling the data, using a diffusion model (P.L. Smith & Ratcliff, 2004) for example, would be one method for dissociating RT effects driven by a bias in stimulus processing from those driven by a bias on a decisional level.

The current study may help us reconcile the seemingly discrepant results produced by traditional BR compared to CFS. Research with CFS, prior to this dissertation, has focused on the processing of high-level visual attributes under suppression. On the other hand, the majority of BR research has focused on relatively early visual processing under suppression. The few BR studies that have investigated high-level processing have found little evidence for its survival under suppression (e.g. Blake, 1988; Cave et al., 1998; van der Zwan, Wenderoth, & Alais, 1993; Zimba & Blake, 1983). In my view, high-level effects reported with CFS may be artifacts from the selective suppression produced by the visual properties of the CFS display. The rival stimulus (suppressor) tends to differ from BR study to BR study and this is mostly due to the fact that stimulus properties strongly influence the duration of dominant and suppressive phases during BR (review by Blake & Logothetis, 2002). The visual features of every BR suppressor have to be well suited for suppressing the stimuli of interest for sufficient periods of time. Thus suppression in BR studies may be more effective at suppressing the particular features of the rival stimuli and in an unbiased manner. In contrast, the majority of CFS studies use the same type of suppressor (e.g. Mondrian-like pattern) and thus the same visual features for suppression. Even the different CFS displays have similar visuo-temporal characteristics (Figure 4.1). Furthermore unlike BR studies, the success of suppression is not monitored online but rather after completion of the main experiment and typically with a sub-optimal task. Regardless of the technique used, it is important that future studies carefully take into consideration the low-level features of the competing stimuli and the level of observers' awareness for the suppressed stimuli.

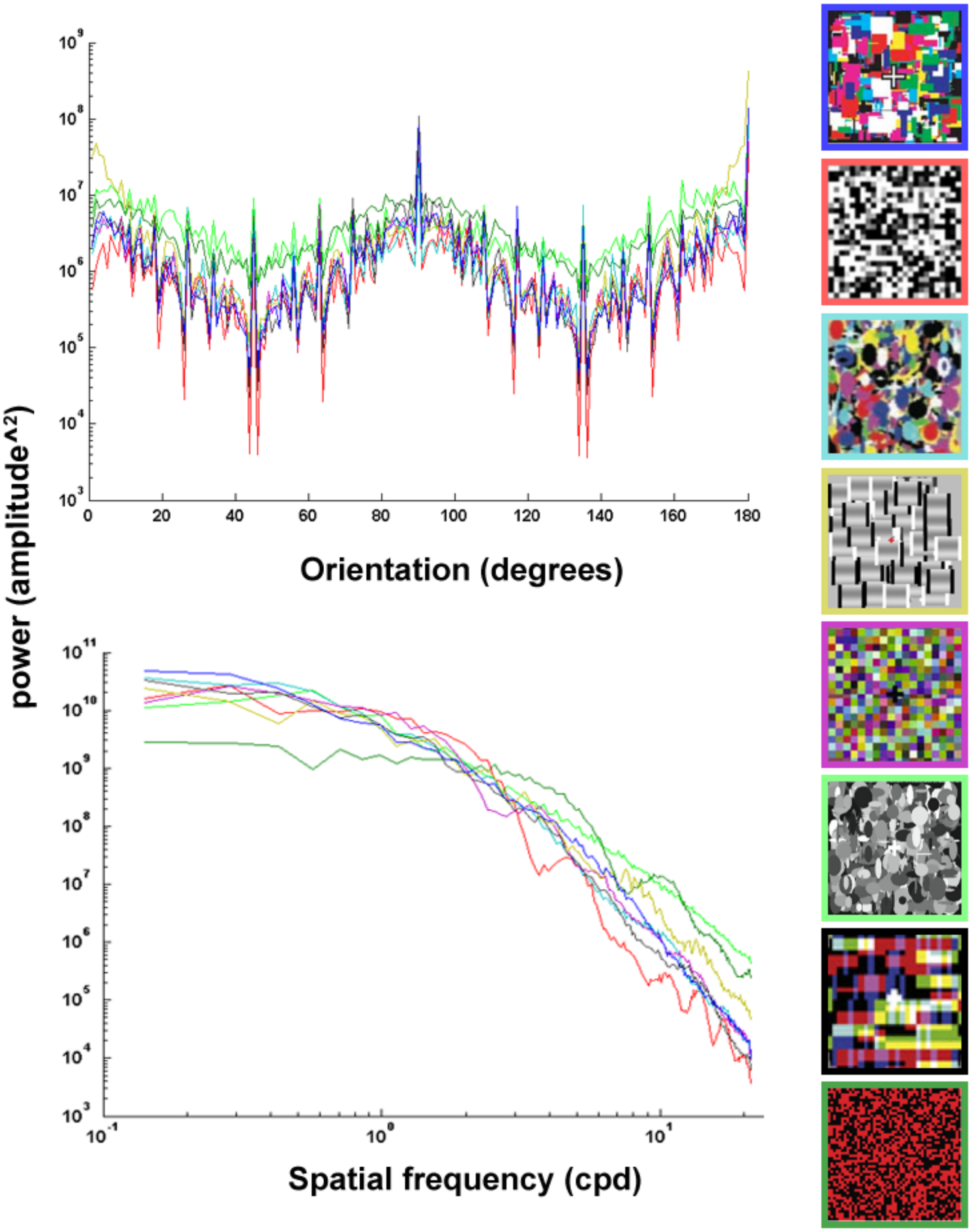

Figure 4.1: The orientation (top) and spatial frequency (bottom) power spectrum of 8 different CFS images of previous studies. Data corresponding to each image is denoted by border color. Images were equated in size (7^{o} x 7^{o}) and contrast (30RMS) prior to be transformed in the Fourier domain. Images were extracted from figures in (top to bottom): Tsuchiya & Koch, 2005; Arnold et al., 2008; Bahrami et al., 2010; Maruya et al., 2008; Costello et al., 2009; Adams et al., 2010; Sterzer et al., 2008; Almedia et al., 2008.

Neural framework for suppression with CFS

Models of BR commonly emphasize reciprocal inhibition between competing neural events as the source of interocular suppression (review by Tong, 2001). Neurons encoding the effectively stronger stimulus will initially inhibit those encoding the competing stimulus, leading to the perceptual dominance of only one image at any given moment. As neurons of the dominant stimulus adapt over time, their inhibitory influence weakens until the balance of activity shifts and inhibition exerted from competing neurons takes over (Alais, Cass, O'Shea, & Blake, 2010). BR models mainly differ in terms of the stage(s) in the visual processing hierarchy that this neural competition transpires (Blake, 1989; Freeman, 2005; Lehky, 1988; Logothetis et al., 1996; Wilson, 2003).

Although it is commonly thought that CFS arises from the same neural events as those underlying rivalry suppression (e.g. Lin & He, 2009), there are some discrepancies between CFS and BR that raise questions about whether binocular rivalry models apply to CFS without refinement. For instance varying the strength of a CFS display lengthens its dominance while its periods of suppression are unaffected (Tsuchiya et al., 2006). This pattern of results is opposite to what is found with BR: increasing the strength of a stimulus decreases its suppression durations without changing its durations of dominance (e.g. Fox & Rasche, 1969; Levelt, 1965; but Bossink, Stalmeier, & De Weert, 1993; Brascamp, van Ee, Noest, Jacobs & van den Berg, 2006; see Kang, 2009, for a review of this literature). To account for the temporal dynamics of CFS, Tsuchiya and Koch (2005) proposed a simple model that incorporates a flash component into the BR model proposed by Levelt (1965). Essentially, every flash component within the CFS display resets its dominance state and the strength of the flash is dependent upon the flash interval, which is most effective between 80 - 320ms (3 - 12 Hz; Tsuchiya and Koch, 2005). In effect, their refinement minimizes the role of neural adaptation of the dominant stimulus, allowing it to maintain its relative strength for considerably longer durations.

Although the model refinement proposed by Tsuchiya and Koch (2005) is sufficient to account for percept durations under CFS, it does not describe the neural mechanisms whereby CFS produces depths of suppression greatly exceeding that associated with conventional BR. Recently, Shimaoka and Kineko (2011) tackled this challenge by expanding the neural model of BR proposed by Wilson (2007) to include CFS. Wilson's BR model incorporates adaptation, reciprocal inhibition and recurrent excitation and is simply composed of 2 equations:

$$\tau \frac{\mathrm{d}E_\mathrm{L}}{\mathrm{d}t} = -E_\mathrm{L} + M[L(t) - aE_\mathrm{R} + \varepsilon E_\mathrm{L} - gH_\mathrm{L}]_+ \tag{1}$$

$$\tau_\mathrm{H} \frac{\mathrm{d}H_\mathrm{L}}{\mathrm{d}t} = -H_\mathrm{L} + E_\mathrm{L} \tag{2}$$

Eq 1 defines the activity level for a monocularly-driven neuron (E_L, L= Left Eye) as the result of input strength (+L(t)), inhibitory strength from the opposing eye ($-aE_R$), recurrent excitatory activity ($+\varepsilon E_L$), and self-adaptation ($-gH_L$). Eq 2 defines the rate of adaptation (H_L). Further details are found in Wilson (2007).

$$\tau \frac{dE_{L1}}{dt} = -E_{L1} + M \cdot \max(L_1(t) - aE_{R1} - a_2E_{R2} - gH_{L1}, 0) \tag{3}$$

Shimaoka and Kineko (2011) incorporated monocular units that are tuned to different stimulus features (e.g. L1, L2, R1 & R2) in order to simulate neural responses to a CFS pattern (Eq 3). Thus, an inhibitory component is added for every feature-selective unit that is responding to input in the opposing eye (e.g. a_2E_{R2} in Eq 3, Figure 4.2 top). The extended model accurately simulates the long dominance durations produced by CFS, as defined by the sum of neural activity of units responding to a stimulus in one eye (Figure 4.2 bottom).

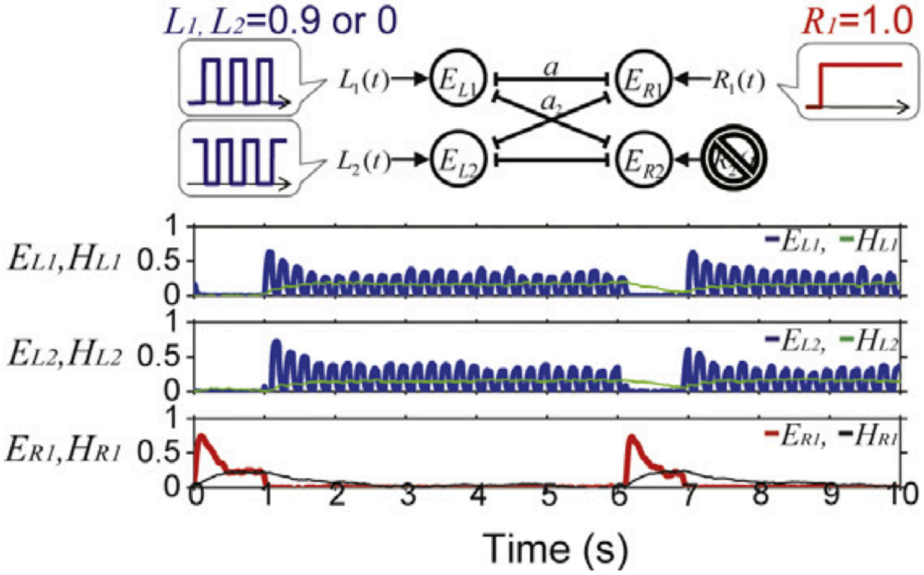

Figure 4.2: Simulation of neural responses based on the extended model by Shimaoka & Kineko (2011). Top illustrates flashing input (e.g. contrast-reverse grating) to left eye and static input to the right eye (L and R = input strength to each eye). Units (E) are tuned to different stimulus features, such as spatial phase in this example. Er2 does not receive input since its preferred stimulus is never presented. a represents reciprocal inhibition among units. Bottom illustrates neural firing of each feature-selective unit (thick lines) and hyperpolarizing current (H; thin lines) indicating the rate of neural adaptation. Illustration was taken from Shimaoka & Kaneko (2011).

With the extended model, Shimaoka and Kineko (2011) attempted to simulate suppression depth with CFS, BR and FS, by simulating results from a probe detection task. Suppression depth was defined as the minimum probe strength that switches dominance from the suppressor to the suppressed stimulus, in which the probe is presented. Figure 4.3 shows that suppression depth with CFS increases (i.e. stronger probe is necessary for a perceptual reversal) as one increases the number of feature-selective units in the model. When there are a large number of units responding to monocular input, probes are more likely to be presented during one of the several transient peak responses. Input to each unit is brief and so adaptation is also low. With fewer units the probe is more likely to appear after transient peak responses have occurred (during the steady-state response), switching the dominant state to that of the probe (Shimaoka & Kineko, 2011).

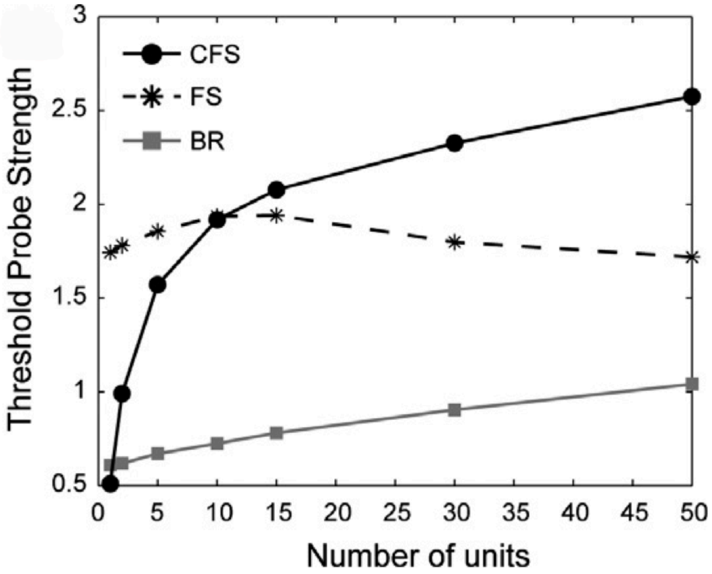

Figure 4.3: Simulation results of a probe detection task with the extended model by Shimaoka & Kineko (2011). The strength of probes presented under CFS, FS, and BR is plotted as a function of the number of feature-selective units. Probe strength ($\beta + \theta^* \exp(-t^2/\sigma^2)$) varied across trials (100 per probe value) while the strengths of the competing stimuli remained constant. Thresholds estimates were based on the probe amplitude at which dominance switched from the suppressor to the suppressed for half of the trials. Details can be found in the original study. Illustration was taken from Shimaoka & Kineko (2011).

At least two additional components are needed in the extended model to account for the findings in this dissertation. If suppression depth is modulated by the visual properties shared between the suppressor and suppressed stimulus, there must be a scaling constant that weights the inhibition from opposing units and is dependent upon their distance in feature space. The result should be strong inhibition from units with similar feature-specific tuning and weak inhibition from units selective for more dissimilar features. Secondly, the current study suggests that there may be a non-linear component to suppression; relatively low spatial frequency and intermediate temporal frequency (~10 Hz) elements produce the strongest suppression regardless of the suppressed stimulus properties. If this bias is attributed to our naturally heightened sensitivity for these components, another variable is necessary to scale the inhibition according to the human spatio-temporal contrast sensitivity function. Inhibition from units tuned to features corresponding to peak sensitivity should be weighted more and features that we are weakly sensitive to should be weighted less. Overall luminance level (scotopic or photopic) will determine the shape of the contrast sensitivity function (Kelly, 1961; Van Nes & Bouman, 1967). Both of these constants would simply weight every inhibitory component in the extended model (e.g. a_1E_{R1}, a_2E_{R2}).

The current findings provide possible clues about the neural sites of suppression. Specifically, my results imply that suppression heavily relies on reciprocal inhibition occurring among detectors selectively tuned to the physical properties of the stimulus. Stuit et al. (2009) observed orientation- and spatial-frequency tuning under rivalry suppression that were similar in bandwidth as those reported in V1 neurons. Similar tuning properties have also been reported within neurons found in extrastriate areas V2, V3, and V4; however, low-level feature-specificity tends to decline along successive stages of processing (e.g. Hubel & Wiesel, 1962 & 1968; Maunsell & Newsome, 1987). Likewise, LGN lacks the necessary orientation response properties (e.g. Hubel & Wiesel, 1961 but Leventhal & Schall, 1983; E.L. Smith, Chino, Ridder, Kitagawa, & Langston, 1990) to yield the current results, but BOLD signal responses measured in LGN do correlate with perception during rivalry, perhaps reflecting an involvement of cortical feedback (Haynes, Deichmann, & Rees, 2005; Wunderlich, Schneider, & Kastner, 2005; but Lehky & Maunsell, 1996). The receptive fields of neurons in V1 can be characterized as spatiotemporal Gabor-like filters, transforming visual input into a Fourier-like representation (e.g., Movshon, Thompson, & Tolhurst, 1978). These filters simultaneously analyze multiple stimulus features and relay information characteristic of magnocellular and parvocellular channels (e.g. Livingstone & Hubel, 1988; Maunsell & Van Essen, 1983; Ungerleider & Mishkin, 1982). The spatio-temporal properties in the CFS display that are most effective in producing suppression are reminiscent of the characteristics that optimally drive the M cells (e.g. Kaplan & Shapley, 1986; Wilson, 1980). This could imply that CFS suppression more strongly attenuates neural activity within the magnocellular pathway, an idea that differs from the view of Lin and He (2009) who propose that it is activity within the parvocellular pathway that is more affected by CFS (see also Hesselmann & Malach, in press).

The involvement of V1 in neural suppression underlying rivalry remains controversial. Single-unit studies in monkeys have reported that the majority of neurons recorded in V1 (as well in V2, V4, and MT) respond robustly and reliably to their preferred stimuli, irrespective of the state of perceptual dominance of those stimuli reported by the monkeys (Keliris, Logothetis, & Tolias, 2010; Leopold & Logothetis, 1996; Logothetis & Schall, 1989). While these studies implicate on-going visual processing in V1 even during perceptual suppression, fMRI studies in humans report that V1 responses are strongly modulated in synchrony with a person's reported perceptual state: fMRI activity is reduced or abolished when the stimulus producing that activity is suppressed under BR (e.g. Haynes & Rees, 2005; Meng, Remus, & Tong, 2005; Tong & Engel, 2001). However, Polonsky, Blake, Braun, and Heeger (2000) showed that the magnitude of V1 responses to the suppressed pattern was reduced by 45-83% in comparison to non-rivalrous stimulus conditions (also Lee & Blake, 2002), implying that neural activity is not completely eliminated by suppression. Furthermore, the reduction in BOLD activity during perceptual suppression seems to be correlated with low-frequency local field potentials but not with spiking activity (Maier et al., 2008). Primate electrophysiology and neuroimaging studies together suggest that signals from the suppressed stimulus undergo some level of processing in V1, although the evidence is less convincing with fMRI.

Only a few studies to date have directly examined whether rivalry suppression involves feature-specific mechanisms, one of which was an fMRI study conducted by Moradi and Heeger (2009). Investigators examined BOLD responses to a pair of compatible (iso-oriented) or incompatible (cross-oriented or plaid) gratings that were presented dichoptically or monocularly to observers. Activity in V1, V2, and V3 showed evidence of stronger interocular suppression with compatible gratings in comparison to incompatible gratings. In other words, inhibitory interactions were stronger among channels tuned to the same orientation than those tuned to orthogonal orientations. These findings resonate well with results of Experiment 2.2 in which suppression was more effective when the CFS and suppressed stimulus shared similar orientation properties. Furthermore, cross-orientation suppression was equally strong under dichoptic (i.e. different gratings to each eye) and monocular (plaid to one eye) conditions, implicating a general mechanism of suppression that is independent of eye of origin (Moradi & Heeger, 2009).

Sengpiel and colleagues (1995a) measured neuronal responses in cat LGN and area 17 tuned to the stimulus presented in the dominant eye as a stimulus of varying orientation and spatial frequency was intermittently presented in the non-dominant eye (i.e. flash suppression). Responses in LGN cells and V1 monocular cells were strongly inhibited by a stimulus flashed in the non-dominant eye, irrespective of the orientation differences between the dichoptically presented stimuli (also Moore, Spear, Kim, & Xue, 1992; Sengpiel, Freeman, & Blakemore, 1995b; but Varela & Singer, 1987). In contrast, inhibition of *binocularly* driven V1 cells was strongly modulated by differences in stimulus orientation; inhibition was strongest when the non-dominant stimulus was orthogonal in orientation whereas iso-oriented stimuli produced facilitation (also Sengpiel & Blakemore, 1994). Thus, orientation-selective suppression is observed in V1 binocular cells but not in LGN or V1 monocular cells and this selective suppression is strongest for dichoptic stimuli that are orthogonally oriented. In Experiment 2.2, the suppressed stimulus was one of 4 orientation bandwidths and 2 bandwidths overlapped with the orientation profile of the CFS display (i.e. cardinally oriented components), which was not manipulated in this experiment. If the suppressed stimulus were composed of only horizontally oriented components, for example, it is possible that the horizontally oriented components of the CFS stimulus resulted in facilitation, whereas its vertically oriented components led to inhibition of neural responses to the suppressed stimulus. This could partially account for the variable pattern of results found across observers in Experiment 2.2 (Figure 2.6). It would be informative in future studies to dissociate the effects of different orientation components in the CFS display, using orientation-band pass filtered CFS images for example.

In contrast, the effects of stimulus spatial frequency observed by Sengpiel et al. (1995a) were quite different. LGN and V1 responses to the dominant stimulus were strongly inhibited when non-dominant stimulus matched in spatial frequency content and inhibition weakened as the spatial frequency difference between the two stimuli increased (also Moore et al., 1992). These results are compatible with the current (Experiment 2.1 & 3.1) and previous findings (e.g. Liu & Schor, 1994; O'Shea et al., 1997; Y. Yang et al., 1992) in which the characteristics of suppression (i.e. depth, duration, exclusivity) varied as a function of the spatial frequency overlap between rival stimuli. Furthermore cat physiology studies, in general, seem to demonstrate both the selective and non-selective nature of interocular suppression, which may represent the role of differently tuned neural populations in suppression. Whether this also pertains to monkey visual cortex we do not know, for comparable physiological studies have not been performed in monkeys.

Limitations of the current study

In the current study, suppression was examined as a function of select regions in the local spatio-temporal feature space defining one version of a CFS display. Spatial frequency and orientation dimensions were explored in particular, since they play a fundamental role in spatial vision and have been well studied in terms of visual sensitivity and underlying neural representation (e.g. Campbell & Kulikowski, 1966; Maffei & Fiorentini, 1973; review by R.L. De Valois & K.K. De Valois, 1980). However, other spatial dimensions are worth exploring such as luminance and color. Luminance and color sensitivity are reported to be differentially affected by suppression (e.g. Hong & Blake, 2009 ; E.L. Smith et al., 1982; Thomas, 1978; but Ridder, Smith, Manny, Herwerth, & Kato, 1992) and recently, Knapen, Kanai, Brascamp, van Boxtel, and Van Ee (2007) showed that exclusivity during BR may also depend on the distance in color space between the competing stimuli. Approximately half of the studies to date have used chromatic CFS displays (see Figure 4.1 for examples), and some researchers claim that suppression is more effective with color (Carmel, Arcaro, Kastner, &

Hasson, 2010) although supportive evidence for that contention, beyond anecdote, is lacking. The temporal frequency domain also warrants further investigation since the current study was limited to examining components associated with the fundamental frequency of 10 Hz, which is most commonly used among CFS studies to date. Findings in the temporal frequency domain may be critical in determining the involvement of specific spatio-temporal channels in suppression and in examining the extent to which spatial frequency-dependent suppression is governed by the temporal characteristics of the CFS display.

If the spatio-temporal components of the CFS display indeed play a significant role in suppression, the current pattern of results may not generalize to findings observed with other CFS displays. As stated earlier, most of the currently utilized displays share similar spatio-temporal characteristics and are typically composed of high contrast, flickering, cardinally-oriented contours (Figure 4.1). The pattern in spatial frequency amplitude spectra for different CFS images is quite similar and follows a power-law function with increasing spatial frequency ($1/f^{\alpha}$), which is common for natural images (e.g., Field and Brady, 1997). Thus the spatial composition of CFS stimuli is not that unusual, and it is likely that similar patterns of selective suppression would be observed with other CFS stimuli.

Concluding remarks

The current study is the first to systematically investigate the characteristics underlying suppression with CFS. CFS operates by selectively attenuating or abolishing certain low-level signals while leaving others to be potentially encoded during suppression. This feature-selective bias in suppression may be attributed to the spatio-temporal properties of the CFS stimulus and the properties shared with the suppressed stimulus. Findings from the current study suggest the involvement feature-selective mechanisms in neural concomitants of suppression. Furthermore, they underscore the importance of considering the contribution of low-level features in stimulus-driven effects that are reported under suppression.

APPENDIX A

SELECTIVITY IN SUPPRESSION USING NATURAL IMAGES AS SUPPRESSED STIMULI

Experiments 2.1 and 3.1 show that CFS greatly impairs observers' sensitivity to low spatial frequency Gabor patches and gratings in comparison to those of high spatial frequency and furthermore, the low spatial frequency components of the CFS patterns is largely what drives this selectivity of suppression. I then wondered whether such selectivity in suppression could be observed with natural images such as faces. In fact, face images are one of the most popular categories of stimuli presented under CFS (e.g. Adams et al., 2010; Fang & He, 2005; Sterzer et al., 2009). As mentioned previously, there are converging lines of evidence to suggest that face processing is not completely squelched under suppression. However, what class of stimulus properties are exactly driving these effects? For instance, behavioral studies have found that upright face images are more likely to emerge from CFS faster than inverted face images (Jiang et al., 2007; E. Yang et al., 2007; G.M. Zhou et al., 2010). However, other studies suggest that these effects may be driven by differences in low-level face properties (Gray et al., 2010) or differences in detection thresholds and response criteria (Stein et al., 2011a) among categories of face images. If CFS suppression is indeed selective for certain spatial frequency components, could the spatial content of a suppressed face also modulate the face inversion effect? The Experiment A attempted to address this question. In a series of experiments, I measured observers' sensitivity to a suppressed face that was either low-pass or high-pass filtered and investigated the face inversion effect using the spatial frequency band-pass technique implemented in Experiment 3.1 and 3.2, with the "time to break suppression" strategy.

Method

Participants

Seven participants, including the investigator, participated in Experiment A. Participants were recruited from the Vanderbilt University Psychology Department and all had normal or corrected-to-normal acuity and good stereopsis. With the exception of the investigator, participants were naïve to the purpose of the study and provided written consent prior to participation.

Apparatus & Stimuli

The apparatus was identical to previous experiments. A set of 500 dynamic Mondrian patterns (4° x 4°, 10 Hz) was randomly generated prior to the beginning of a block of trials. A subset was randomly chosen for each trial. The RMS contrast of the Mondrian patterns was normalized to 15% for Phases 1 and 2 and 60% for Phase 3. Two face images with neutral expressions were selected from the Karolinska Database of Emotional Faces (Lundqvist & Litton, 1998). Face stimuli were cropped to remove features outside of the face (2° x 1.5°) and were then scaled to gray and normalized in contrast (50% RMS contrast) and mean luminance. The procedure for band-pass filtering was identical to the procedure used in Experiment 3.1 for Mondrian patterns and Experiment 3.2 for probe stimuli. The center frequency for the low-pass and high-pass filter was 0.75 cpd and 6 cpd, with an octave wide bandwidth. The band-pass filtered stimuli were then normalized in contrast (50% RMS contrast) and mean luminance and embedded in 1D broadband Gaussian noise (4° x 4°, 10% RMS contrast). Face stimuli were always presented upright in Phases 1 and 2, whereas in Phase 3 the face stimuli were either upright or inverted 180°. The distance from the face stimulus center and the center of the background noise (fixation) was approximately 1° and across trials, the face stimulus was randomly positioned in one of the two vertical halves of the background noise (Figure A.1). Binocular fusion contours (4.1° x 4.1°) surrounding the stimuli and fixation dots were present at all times to promote stable binocular eye alignment.

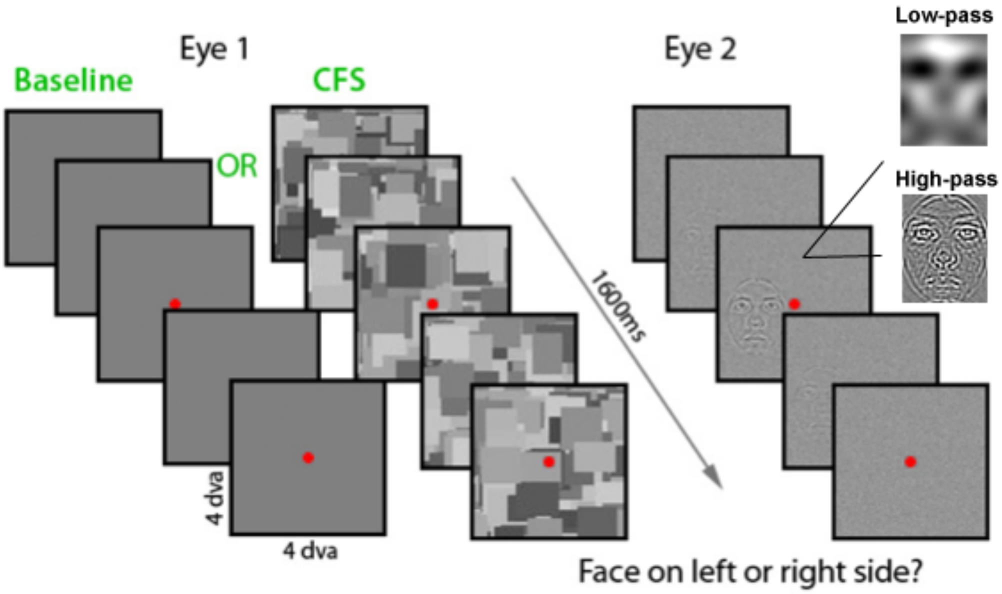

Figure A.1: Illustration of a trial sequence in Experiment A.

Procedure

Experiment A consisted of 3 phases. In the first 2 phases, contrast threshold estimates for detecting low-pass and high-pass filtered faces were obtained in the presence and absence of CFS (baseline). In the final phase, I measured the time it took for the same band-pass filtered faces to emerge from suppression when they were upright or inverted and equated for effective contrast.

In each trial of Phases 1 and 2, a band-pass face stimulus was presented to the dominant eye. The non-dominant eye viewed a dynamic CFS display or a uniform gray field in Phase 1 and Phase 2, respectively. The contrast of the face stimulus linearly ramped on and off during the first and last 300 ms of the trial in order to avoid abrupt transients. For 1 s, the face stimulus remained at a set contrast predetermined by the QUEST adaptive staircase procedure. The face stimulus was presented either in the left or right half of the noise display. At the end of the 1.6 s trial, the stimuli were replaced with a mask, which signaled to observers that a response had to be made regarding the location of the face stimulus (left or right). No feedback was given and the subsequent trial began 250 ms after a response was made. Eight contrast threshold estimates corresponding to 72% performance accuracy were obtained for each band-pass condition, using QUEST. Four staircases of the same condition were randomly interleaved within a block of trials (4 blocks total). Phases 1 and 2 each took approximately 45 minutes to complete.

The procedure for Phase 3 was adapted from previous studies in which investigators measured the duration in which stimuli emerged from suppression (e.g. Jiang et al., 2007; E. Yang et al., 2007; G.M. Zhou et al., 2010). In the initial 1000 ms, the non-dominant eye was presented with a high contrast dynamic CFS display (60% RMS contrast) and the other eye viewed the band-pass face stimulus, the contrast of which linearly increased in order to avoid abrupt transients. The orientation of the face image was either upright or inverted 180°. The full contrast of the face stimulus was the respective mean threshold contrast obtained in Phase 1 for that particular band-pass image. Once the face stimulus reached full contrast (1 s), the CFS display linearly decreased in contrast with every change in pattern (10 Hz) for the remaining 9 s of the trial. Observers were instructed to respond as soon as they could determine the location of the face (left or right), using 1 of 2 keys. RT and accuracy were recorded. The trial terminated either when a response was made or when the CFS display reached 0 contrast. If a response was not made within the trial duration (10 s), that trial was removed from analysis. Observers were discouraged to make guesses and received feedback if an incorrect response was made. A mask stimulus was presented dioptically for 500 ms once the trial ended and the next trial began after 250 ms. Each face orientation condition (upright or inverted) consisted of 200 trials and a low-pass (2) or high-pass (2) filtered face image was presented in half the trials. Trials of each orientation and band-pass filter condition were randomized in order. Phase 3 took approximately 30 minutes to complete.

Results & Discussion

In Phases 1 and 2, contrast detection threshold estimates were measured for high- and low-bandpass filtered face images that were in the presence or absence of CFS. A 2 x 2 repeated measures ANOVA on threshold estimates revealed a main effect of phase (F(1,6)=26.6, *p*=.002, η_p^2=0.8) and an interaction between phase and spatial frequency condition (F(1,6)=7.0; *p*=.04, η_p^2=0.5). Similarly done with previous experiments, elevations in contrast thresholds were computed as the log ratio of the mean threshold estimate for detecting a given band-pass filtered face under CFS (Phase 1) to the mean baseline threshold estimate for detecting that same face without CFS (Phase 2). The left graph in Figure A.2 shows that CFS produced greater elevation in thresholds to low spatial frequency bandpass filtered faces relative to high-pass filtered faces (mean ± SEM: low-pass: 0.87 ± 0.07; high-pass: 0.44 ± 0.04, t(6)=11.8, *p*<.001), replicating Experiment 2.1 and Experiment 3.1. Furthermore, threshold elevations were similar in magnitude as those found with Gabor patches in Experiment 2.1 (see Figure 2.4; 1 cpd = 0.85 log units, 4 - 8 cpd= 0.4-0.2 log units).

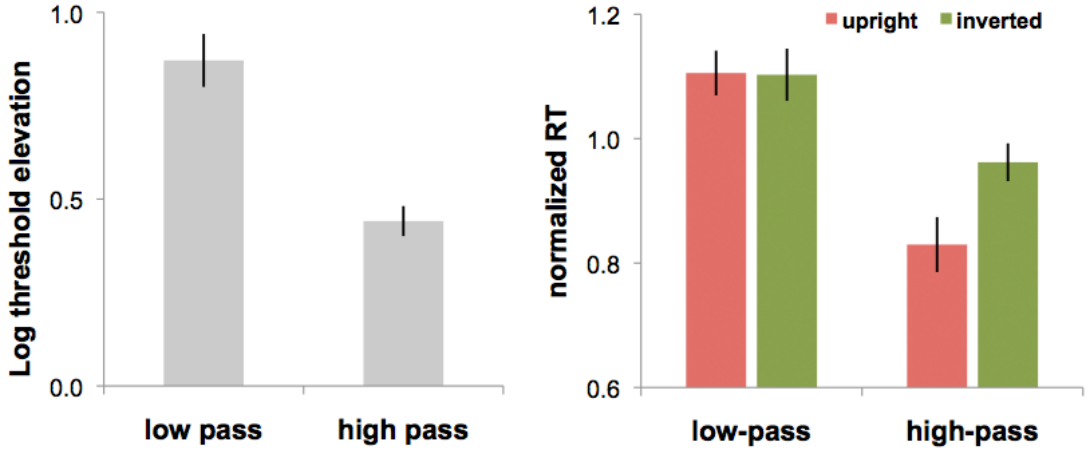

Figure A.2: Results of Experiment A. Left: Elevation in contrast thresholds for detecting low-pass and high-pass filtered face images under CFS, relative to baseline (Phases 1 & 2). Right: Normalized mean RT for detecting low-pass and high-pass faces that were upright or inverted under suppression (Phase 3). Error bars denote SEM.

In Phase 3, observers indicated the moment at which the face stimulus broke suppression and became visible. There were no significant differences in mean accuracy in terms of the face orientation or the spatial frequency filter applied to the face images. Overall mean performance was high (97.5% ± 0.76), suggesting that observers were careful to respond on the basis of the emergence of a face into dominance.

Mean RTs for each bandpass filter and face orientation condition were normalized to the mean RT for that observer (Figure A.2, right). A 2 x 2 repeated measures ANOVA on normalized mean RT values revealed a significant main effect of bandpass filter (F(1,6)=8.6, *p*=.03, η_p^2=0.6) and a significant interaction between bandpass filter and face orientation (F(1,6)=37.7, *p*=.001, η_p^2=.86). The main effect of face orientation was approaching significance (F(1,6)=5.2, *p*=0.06, η_p^2=0.46). Post hoc analysis using paired sample t-tests showed no significant difference in normalized RTs for detecting upright low-pass faces versus inverted low-pass faces (*p*>.05). In contrast, observers were significantly slower to detect an inverted high-pass filtered face relative to its upright counterpart (0.13 ± 0.03, t(6)=4.8, *p*=.003); the mean latency difference was approximately 530 ms (SEM: 150 ms).

As illustrated in Figure A.2, RTs were overall slower for low-pass filtered faces in comparison to high-pass filtered faces (mean difference in RT: 960 ms). This could suggest that low-pass faces were more difficult to detect than high-pass faces even though faces were all presented at their respective mean threshold contrast corresponding to 72% performance accuracy. Nonetheless, observers' mean RT for low-pass faces (4.4 s ± .62) is well below the maximum RT that could be measured within a trial (10 s), which implies there was no ceiling effect.

Experiment A showed that suppression evoked by CFS greatly attenuates contrast sensitivity to the low spatial frequency components (0.5 - 1 cpd) of an image of a face relative to high spatial frequency components (4 - 8 cpd) of a face image. These results are consistent with contrast threshold elevations observed with Gabor patches in Experiment 2.1 and with gratings in 2.2. Furthermore, faces tended to emerge from suppression faster when they are upright as opposed to inverted in orientation, replicating previous studies. However, this face inversion effect appears specific to high spatial frequency features of the face. This could imply that, due to the selective nature of CFS suppression, previous behavioral evidence of face inversion effects under CFS could solely driven by high spatial frequency components in the suppressed face.

APPENDIX B

REPLICATION OF EXPERIMENT 3.1 USING DIFFERENT PARAMETERS

The results of Experiment 3.1 showed that the differential impairment in contrast sensitivity in the spatial frequency domain (Experiment 2.1) is modulated by the spatial frequency components of the CFS display. That is, stimuli composed solely of low spatial frequencies are suppressed more strongly than those of high spatial frequencies with unfiltered CFS. The pattern in threshold elevation observed with unfiltered CFS can be reproduced using CFS displays composed solely of low spatial frequency information. As the CFS band-pass filter shifted towards high spatial frequencies, the bias in suppression of low spatial frequencies weakened and suppression overall grew shallow. In Experiment B, I examined whether these results can be generalized across experimental designs with different spatial and temporal stimulus parameters.

Method

The major differences in design between this experiment and Experiment 3.1 are that stimuli were smaller in size (2° x 2° vs 4° x 4°), stimuli were presented for double the duration (1200 ms vs 600 ms) and the range in spatial frequencies of the target stimulus and CFS display differed (see below). The procedure and design of this experiment (with the exception of the filtered CFS conditions) is identical to those of Experiment 2.1, in which contrast threshold elevations were estimated for 6 different spatial frequency gratings that were suppressed solely by unfiltered CFS displays. Three participants from Experiment 2.1, including the investigator, were recruited. The spatial frequency of the target stimuli (Gabor patches) were 0.5, 1, 2, 4, 8, or 12 cpd. The CFS display was a set of dynamic Mondrian patterns (2° x 2°, 10 Hz) randomly generated prior to the beginning of a trial. These patterns were filtered in a similar manner as those in Experiment 3.1. The center frequency of the bandpass filter was either 0.5, 1, 2, 4, 8, or 16 cpd, with an octave wide bandwidth. All band-pass filtered Mondrian images were normalized in contrast (15% RMS contrast) and mean luminance. Please refer to Experiment 2.1 for details of the procedure. Observers performed a 2AFC orientation discrimination task on Gabor stimuli presented under CFS. There were 36 conditions (6 Gabor spatial frequencies x 6 bandpass filtered CFS displays) and 4 contrast thresholds were measured for each condition, using QUEST. Each staircase consisted of 40 trials and two staircases of the same condition were randomly interleaved within a block of trials. Observers participated in 4 sessions and each session consisted of 18 randomly chosen conditions (36 staircases). A session took approximately 60-90 minutes to complete.

Results & Discussion

Elevations in contrast thresholds were computed in an identical fashion as previous experiments and were entered into a 6 (CFS filter) x 6 (gabor spatial frequency) repeated measures ANOVA. The main effects of CFS spatial frequency (F(5,10)=14.5, *p*<.001; η_p^2=0.88) and gabor spatial frequency (F(5,10)=31.4, *p*<.001; η_p^2=0.94) on threshold elevation were significant. More important was the significant interaction between the spatial frequency conditions of the rival stimuli (F(25,50)=9.3, *p*<.001; η_p^2=0.8). Figure B.1 clearly shows a similar pattern in contrast threshold elevation as the results of Experiment 3.1 (compare with Figure 2.6). Elevations in contrast thresholds resulting from low-pass filtered CFS (center frequency: 0.5-4 cpd) produced elevated thresholds similar to those measured when the CFS was unfiltered (data obtained from Experiment 2.1). High-pass filtered CFS (8-16 cpd), however, produced very little elevation in thresholds, despite the fact that they were equated in contrast to low-pass filtered CFS (15% RMS contrast). And so observers' contrast sensitivity under these conditions were similar to that obtained in the absence of CFS (baseline). Results of Experiment B confirm that the low spatial frequency properties of the CFS display strongly modulate the selective suppression observed for low spatial frequency information presented to the other eye.

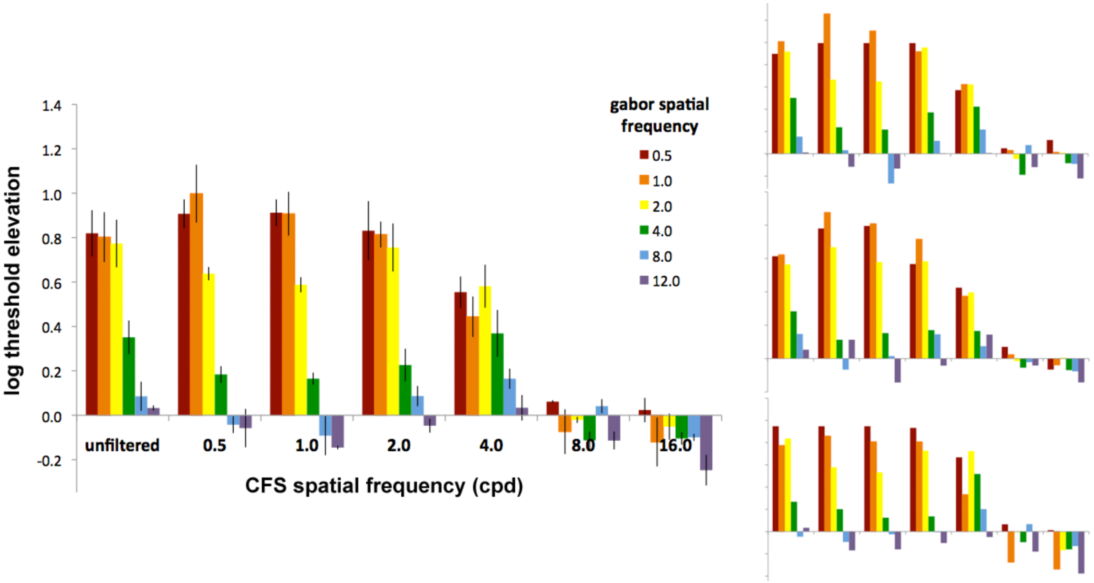

Figure B.1: Results of Experiment B. Group (left) and individual (right) log threshold elevations for detecting a gabor patch of given spatial frequency (bar color) is plotted as a function of the CFS spatial frequency bandpass filter. Note that the data for the unfiltered CFS display is data obtained from the same 3 observers from Experiment 2.1.

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